HAND MOVEMENTS REVEAL THE TEMPORAL CHARACTERISTICS OF VISUAL ATTENTION

by

PHILIP JAMES WILLIAM WOODGATE

A thesis submitted to the University of Birmingham for the degree of DOCTOR OF PHILOSOPHY.

School of Psychology

College of Life and Environmental Sciences

University of Birmingham

November 2014

Abstract

This thesis applied a choice reaching task (CRT) to different visual search settings to investigate the temporal characteristics of visual attention. The initiation latency (IL) and maximum deviation (MD) of the reach trajectory provided the greatest insight into early and ongoing competition for selection. We replicated priming of pop-out (PoP) effects on IL and MD before using the PoP paradigm to examine motor system involvement in generating movement-relevant predictions. Predictable repetition of the target colour recruited the motor cortex but only when the colour signalled the target of an overt movement. We also demonstrated that reaches are affected by global-to-local scene processing presenting a novel dissociation of IL and MD. IL reflected global configural biases (bottom-up), whilst MD reflected local positional biases (top-down). Finally, we examined the influence of irrelevant features (IFs) on target selection. Attentional capture by the IF affected the entire selection process when the target colour and IF presence were unpredictable. When the IF could coincide with multiple search items performance was modulated by early proximity and late similarity grouping. Overall, the results demonstrate the ability of the CRT to investigate the time course of attentional processing above and beyond that provided by key-press response tasks.

Acknowledgements

I would like to thank my supervisor, Dietmar Heinke, for his ever-patient guidance and advice. This body of work would have been an impossible task without his considerable input.

I am grateful to my friends throughout the department, both old and new, for being there to share the many ups and downs of research. A special mention goes to kindred spirits Darren and Steve, mainly for sharing in the solace of football, cricket and beer. Thanks also, to my friends outside of the research world for providing regular doses of laughter and perspective.

I am blessed with the most wonderful family. Thank you to my parents, Graham and Elaine, and to Sarah and Robert, for their love and support – both emotional and financial. Without them I would never have embarked upon this journey let alone completed it. Finally, a special thank you to my girlfriend, Hayley. Her constant love and encouragement is my driving force. I couldn't have done this without her.

Table of Contents

Table of Contents

Table of Contents

Table of Contents

List of Figures

List of Figures

List of Tables

CHAPTER 1

General Introduction

1.1 Introduction

The visual environment is a complex place. Put simply, there is too much information for us to be able to process at any one time. Selective attention enables us to filter this information and select the most important aspects of the visual scene for further processing. Being able to target one item whilst ignoring numerous distracting items is critical for executing the simplest of tasks; imagine searching for your favourite pen in a drawer full of stationary, a familiar face in a crowded photograph, or the lone red sock in a load of white washing. The present thesis examines how this crucial orienting of attention to target items can be modulated by biases such as priming of pop-out (PoP), the configuration of the search items, and the presence of irrelevant features (IFs). We will also use the PoP paradigm to probe the involvement of the motor cortex in expectation-based guidance of target selection. The studies presented are all linked by a common methodology: the choice-reaching task (CRT). The CRT uses the leakage of cognitive processing into motor output to examine the time course of target selection in greater detail (see Song & Nakayama, 2009; for a review).

1.2 Visual search

Research investigating the selection of a target item amongst competing stimuli typically uses a visual search paradigm (see Eckstein, 2011; and Müller & Krummenacher, 2006; for reviews). In a feature search experiment (as opposed to a conjunction search task) an array of stimuli are presented on a visual display with the participant required to complete one of two tasks. In a target detection task the participant is instructed to press "A/B" if the target is present/absent. In a target discrimination, or compound search task, the participant must press "A/B" depending on some feature of the target item (such as the location of a cut-off segment, e.g. Maljkovic & Nakayama, 1994, 1996). The target is usually defined as the 'odd-one-out'

along a particular dimension such as colour, size, shape, orientation, motion etc. The ease with which the participant selects the target and, if necessary, processes a feature of the target, is inferred from the time taken to make the key-press response.

1.2.1 Perceptual priming

Maljkovic and Nakayama (1994) presented a seminal series of studies that examined the effects of target repetition. In their priming of pop-out (PoP) paradigm the participant completed a compound search task discriminating the location of a cut-off segment on an odd-colour target. Their first experiment found that when target colour changed unpredictably from trial-to-trial (mixed condition) reaction times (RTs) were longer than when target colour remained constant (blocked condition). This shows the facilitatory impact of top-down knowledge of the target colour on search performance. This PoP effect is not observed when a target detection decision is required rather than a discrimination decision (Bravo & Nakayama, 1992) showing the PoP effect relies on focal rather than distributed attention. Moreover, performance in the mixed condition was facilitated by increasing the number of distractors. The effect of distractor number was absent in the blocked condition. This suggests that when target identity is unpredictable the bottom-up contrast of the search items drives target discrimination. With more distractors the contrast with the target increases and the target 'pops-out' more efficiently (see also, Bravo & Nakayama, 1992).

In subsequent experiments Maljkovic and Nakayama (1994) demonstrated that the PoP effect endures regardless of the hemifield in which the target is presented, the contrast between target and distractors, and despite the prime and the current presentation being separated by several trials. More importantly, the PoP effect accumulated over a streak of target colour repetitions – the reduction in RTs was greatest after one repetition but RTs

continued to decrease until performance matched that of the blocked condition after eight repetitions.

Such key-press tasks have undoubtedly increased our understanding of target selection and the biases thereon. Recently, key-press tasks have been combined with eye-tracking paradigms so that a better understanding of *how* the distractors are influencing search can be attained (e.g. Rutishauser & Koch, 2007; Zelinsky, Rao, Hayhoe, & Ballard, 1997). For example, McPeek, Skavenski, and Nakayama (2000) showed that when target colour changes following a streak of repetitions initial saccades are made towards a distracting item but are often corrected to fixate the target within 10-100ms. This rapid re-fixation suggests that the corrective second saccade is planned in parallel with the initial incorrect response. Eye-movement research has also examined the curvature of saccades when completing search tasks (e.g. McPeek & Keller, 2001). However, the rapid, ballistic nature of eye-movements allows only a very brief insight into the ongoing competition between target and distractors.

1.3 The choice reaching task

Song and Nakayama (2006) developed the CRT as a way of gaining greater insight into the time course of target selection. CRTs have uncovered continuous influences on attentional processing, including, PoP (Chapter 2; Song & Nakayama, 2006), target-distractor competition (Chapter 2; Song & Nakayama, 2008), global-to-local scene processing (Chapter 4), and irrelevant feature interference (Chapters 5 & 6), as well as biases on other cognitive domains, such as, language processing (Dale, Kehoe, & Spivey, 2007; Spivey, Grosjean, & Knoblich, 2005), numerical representation (Song & Nakayama, 2008), and complex decision making (McKinstry, Dale, & Spivey, 2008). The following introduces Song & Nakayama's

CRT experiments focusing on the CRT's theoretical basis and its ability to index ongoing competition for focal attention.

1.3.1 Song & Nakayama's experiments

Insight into cognitive processes is possible due to the dynamic and parallel operation of perception, cognition and action – the 'leakage' of ongoing processing into motor output offers a window into cognitive operations and their temporal priority. In a visual search setting the ongoing processing translates into continuous competition between search items, consistent with Desimone and Duncan's (1995) biased competition theory. The items on the screen compete for activation and are selected once a decision threshold is passed. In the CRT participants are asked to reach and touch a target amongst distracting items as quickly and as accurately as possible. There are two main outcome measures: the time taken to start the reach following stimulus onset (*initiation latency*) and the deviation of the reach trajectory from the ideal path (i.e. a straight line between reach start and end; *maximum deviation*). Importantly, the CRT is based on the assumption that activation can be accumulated by all stimuli in parallel (see Cisek and Kalaska (2002, 2005) for evidence that the dorsal premotor cortex (PMd) simultaneously represents target and distractor positions). Therefore, if a distractor achieves the threshold prior to the target the reach is initiated toward that distractor and must be corrected midflight, resulting in greater trajectory deviation.

1.3.1.1 Song & Nakayama (2007). The threshold at which the decision is made is reflected in the initiation latency (IL) of the movement. Song and Nakayama (2007) showed that when easy single target trials are presented in a block this threshold was reduced and the movement started earlier. However, when single target and more difficult odd-colour search trials were randomly intermixed the initiation threshold could not be adjusted from trial-to-trial. Thus,

the threshold was homogenised between the levels of the easy and hard trials (the *visuomotor hypothesis*). The subsequent reduction of latencies for difficult, odd-colour search trials increased the chances of selecting a distractor and resulted in increased maximum deviation (MD) compared to single target trials.

1.3.1.2 Song & Nakayama (2006). As shown by Maljkovic and Nakayama (1994; see 1.2.1) discrimination of a target feature relies upon the deployment of focal attention to the target item. If it did not, and distributed attention was sufficient for discrimination, then we would not see a reduction in RTs with target colour repetition (PoP), nor a facilitatory effect of increased distractor numbers when the target colour varied from trial-to-trial. If reaching and touching the target shows the same pattern of effects then it is safe to conclude that the CRT is also able to index focal attention. Song and Nakayama (2006) showed this to be the case. In the blocked condition (predictable target colour) IL and MD were unaffected by the number of distractors present. In the mixed condition (unpredictable target colour) IL and MD were increased compared to the blocked condition and were modulated by the number of distractors present. With just two distractors performance was worse compared to displays with five and eleven distractors. Thus, reaching movements were influenced by both PoP – improved performance in the blocked versus mixed condition – and perceptual grouping – improved performance with increased distractor numbers. In a second experiment Song and Nakayama (2006) probed the number of target colour repetitions needed to produce a significant improvement in reach performance. They found that IL showed a gradual reduction over six colour repetitions whilst MD showed a large reduction after just one repetition before plateau. Thus, consistent with previous key-press (e.g. Maljkovic & Nakayama, 1994) and eye-movement studies (McPeek et al., 2000) manual reaching movements are also reliant on focal attention that can be manipulated by biases such as priming and grouping.

1.3.1.3 Song & Nakayama (2008). In a separate experiment Song and Nakayama (2008) scrutinised the characteristics of reaches that exhibited curved trajectories. Curved trajectories showed no overall time cost compared to straight trajectories (when IL is combined with *movement duration*, or, the time spent moving the hand to the target). Although curved reaches had longer movement duration than straight reaches the shorter IL of curved reaches compensated for this increase. Song and Nakayama (2008) then investigated how curved reach movements were able to maintain the same efficiency as straight movements despite initially selecting a distractor. By comparing the time at which the maximum deviation occurred (i.e. the onset of the corrective movement towards the target) with the IL of the movement they showed that the average IL was approximately 300ms, yet the corrective movement began approximately 125ms into the initial movement. In order to execute the corrective movement toward the target so soon after reach onset (i.e. in less time than it took to begin the initial movement) the initial incorrect movement and the later corrective movement must have been planned in parallel prior to movement onset (again consistent with neurophysiological evidence of Cisek and Kalaska (2002, 2005)).

1.3.2 Outlook

The goal of Chapter 2 in this thesis was to build on these initial results. For instance, are there any reach parameters other than timing and trajectory deviation that offer further insight into the selection process? The main candidates considered are the time of maximum deviation, peak velocity, the time of peak velocity and the number of velocity peaks. The time at which maximum deviation occurs has surprisingly been overlooked in previous CRT research given the strong temporal aspect of the task. Likewise, the aforementioned peak velocity variables are well defined when reaching to single targets (Jeannerod, 1988) and towards targets

amongst distractors (Keulen, Adam, Fischer, Kuipers, & Jolles, 2004) enabling clear interpretation of the effects of our experimental manipulations. Furthermore, it is clear distracting items cause trajectory deviation but where does the reach initially deviate towards? An analysis of initial movement direction will hopefully go some way to answering this question. Finally, Chapter 2 also presents an attempt to replicate Song and Nakayama's (2006) findings of PoP effects on IL and MD. Chapter 3 will then go on to apply the PoP paradigm to investigate the role of the motor cortex in target prediction.

1.4. The motor system & target prediction

Traditional models of the motor system assume that it 'simply' has to read out previous processing to execute a movement to a target defined by visual attention (e.g. Marr, 1980; Sternberg, 1969). Recently, however, such serial models have been questioned by research showing motor system involvement in visual processing via feedback connections to earlier areas, including the posterior parietal cortex (PPC; see Brown, Wilson, Goodale, & Gribble, 2007; Hecht, Vogt, & Prinz, 2001; Ostry, Darainy, Mattar, Wong, & Gribble, 2010). This research highlights the transfer of learning between action and perception can be bi-directional. Most important in the context of this discussion is research showing motor cortex involvement in the formation of expectations of perceptual information. Schubotz and von Cramon (2002) conducted an fMRI experiment where participants were asked to predict the size of an upcoming square based on a preceding sequence of squares. The prediction of size activated the premotor cortex as well as supplementary motor area and intraparietal sulci (located within the PPC). Moreover, there is also evidence that the motor system can represent statistical information about visual stimuli. When a visual target is instructed by a reliable visual cue corticospinal excitability (CSE; elicited by transcranial magnetic

stimulation (TMS) over the motor cortex) has been shown to increase accordingly prior to the onset of the target. Conversely when the cue failed to accurately predict the visual target CSE was reduced (Bestmann, Harrison, Blankenburg, Mars, Haggard, et al. 2008). This suggests that the motor system is sensitive to statistical relationships, in this case the degree of (un)certainty surrounding a particular target.

Taken together this evidence suggests that the motor system may act as a predictor of perceptual events (see also Schubotz, 2007). The PoP effect can also be viewed as relying on implicit prediction: the expectation of a target colour repeat facilitates the deployment of focal attention to the same colour item. Hence, it is possible that the statistical architecture of the PoP paradigm may recruit the motor system. Motor cortex involvement may be particularly plausible in the CRT where the target colour signals the location of an overt movement target. This prediction will be tested in Chapter 3.

1.5 Time course of scene processing

As noted, the continuous nature of the CRT is ideal for probing the timeline of cognitive processing. Until now the discussion has focused on the ability of the CRT to uncover colour PoP effects and their influence on motor system activity. Another aim of this thesis is to examine whether visually-guided reaching movements are affected by the cascade of visual processing from global- to local-levels.

1.5.1 Global-to-local processing

It is generally assumed that visual scenes are processed in a global-to-local fashion. This means that the global properties of the display emerge prior to the local-level features. Support for this theory is provided by numerous behavioural studies across a wide array of

cognitive domains (see Hegde, 2008; for a review). For instance, in Navon's (1977) classic hierarchical figures paradigm participants are presented with a large (i.e. global) letter comprised of smaller (i.e. local) letters. RTs for identifying the global letter are faster than for the local letter. Moreover, incongruence between the large and small letters disrupts identification of the local letter but not the global letter. Both of these findings indicate that the global information is processed prior to the local information (see also Schyns and Oliva, 1994; for evidence of analogous coarse-to-fine processing of visual scenes). Furthermore, face processing researchers have long distinguished rapid identification of faces based on configural processing – e.g. the presence of the eyes above a nose above a mouth – from slower discrimination based on processing of individual features (see Maurer, Le Grand, & Mondloch, 2002; for a review).

Such behavioural studies have been complemented by neurophysiological investigations revealing the neural progression of processing from global- to local-levels. For example, Conci, Töllner, Leszczynski, and Müller (2011) showed that global targets evoked larger ERPs in early sensory components and that attentional orienting to a globally-defined target occurred approximately 70ms earlier than with local-level targets. However the behavioural evidence for global-to-local processing stems from key-press response tasks that often require changes in task demands. For instance, in Navon's (1977) paradigm participants are explicitly instructed to respond to the global- or local-level letter from one block of trials to another. There is strong evidence that changing task requirements can disrupt normal processing, even reversing the cascade of global-to-local processing (see Hübner & Volberg, 2005). Grice, Canham, and Boroughs (1983) showed that when participant's fixations were restricted the precedence of the global letter over the local letter was eradicated, although global precedence could be reinstated by peripheral presentation of the compound letter (see

also Caparos, Linnell, Bremner, de Fockert, & Davidoff, 2013; for cross-cultural differences in susceptibility to Navon-style task-demands).

1.5.2 Global-to-local processing & the choice reaching task

If we are able to investigate the global-to-local processing strategy using the CRT we can overcome such task-setting biases. We predict that the initiation of the movement (IL) should be affected by global processing whilst the later movement phase (MD) should be influenced by local processing. This is based simply on the temporal coincidence of IL with early processing and MD with later processing. It will be interesting to observe whether the CRT is flexible enough to index biases on global level as well as local level processing when the task encodes such a progression of processing. To operationalise global and local scene processing we will prime the configuration of the search items (global) and the position of the target (local). Importantly, task requirements (i.e. reach and touch the odd-colour item) will remain the same throughout the experiment. We expect that repeating the configuration of the search items will reduce ILs. On the other hand MD should be reduced when the target position repeats, increased when the target appears at a previous distractor location, and remain the same when the target is presented at a previous empty location. This position priming pattern has previously been demonstrated in local-level key press response tasks (e.g. Geyer & Müller, 2009; Maljkovic & Nakayama, 1996). We expected the CRT to be able to index position priming based on Song and Nakayama's (2006) work showing local-level colour priming effects on MD and IL (see 1.3.1.2). We will utilise position, rather than colour priming because colour priming may still produce global structures by grouping the two distractors according to colour. Hence, position priming allows a clearer investigation of local-level processing. It is important to note the novelty of the proposed IL-MD dissociation

with respect to Song and Nakayama's (2006) study. By using only one display configuration Song and Nakayama's (2006) effects were deliberately restricted to the local-level (i.e. focal attention). If we are able to show global-level effects on IL by introducing a second configuration it would demonstrate the utility of the CRT for tapping into early and late cognitive processes.

1.6 Interference in target selection by irrelevant features

1.6.1 Top-down versus bottom-up processing

A central debate within the field of attention concerns the reliance on bottom-up versus top-down processes when selecting a visual target (e.g. Cave & Wolfe, 1990; Corbetta & Shulman, 2002; Egeth & Yantis, 1997; Wolfe, Cave & Franzel, 1989). Top-down processes are driven by internal factors such as an individual's goals and selection biases. Conversely, bottom-up, or stimulus-driven processing, relies on external, physical salience signals. This applies to feature search tasks where the target effortlessly 'pops-out' from the distractors (e.g. Maljkovic and Nakayama, 1994). Accordingly, if a distractor salient along a task-irrelevant dimension (e.g. a large distractor in a colour-defined search task) exerts an influence on target selection then we can conclude that this distractor has captured attention in a bottom-up fashion.

Probing the dichotomy between bottom-up and top-down processes has produced a wealth of studies that have advanced our understanding of target selection (see Theeuwes, Olivers, & Belopolsky, 2010; for a review). Recently however, the view that stimulus- and goal-driven mechanisms operate in isolation from each other has come to be outdated (Awh Belopolsky, & Theeuwes, 2012). Rather, the focus has switched to how the two mechanisms interact and the circumstances under which one is more dominant than the other.

1.6.2 Irrelevant feature interference

In our visual environment targets of our attention can typically be separated from distracting items along more than one dimension. For instance, successful search for a blue pen amongst black pens may also have to overcome differences in size or shape of the pens. This is investigated in the laboratory using a search paradigm where an item is presented that is salient along a dimension other than that which separates the target from the distractors. Such a paradigm is referred to as an *additional singleton* task when the salient singleton is able to coincide with a distractor (e.g. Zehetleitner, Proulx & Müller, 2009), or an *irrelevant feature* task when the salient singleton can coincide with either the target or a distractor (e.g. Proulx, 2010). For simplicity, throughout this thesis the salient singleton will be referred to as an irrelevant feature (IF).

Disruption of search performance by an IF has been reported on numerous occasions (e.g. Proulx, 2010; Theeuwes, 1992; Turatto & Galfano, 2001; Zehetleitner et al., 2009). Such IF disruption must be due to bottom-up 'attentional capture', that is, the attentional system is unable to 'ignore' the IF because it contrasts with the other stimuli, even though it offers no information that facilitates target selection. Accordingly, any processes that can attenuate capture effects must be top-down in nature. Thus, research that investigates the conditions that lead to IF attentional capture and those that lead to the attenuation of capture are able to infer the relative importance of bottom-up versus top-down processing (e.g. Anderson, Laurent, & Yantis, 2011; Ansorge, Kiss, Worschech, & Eimer, 2011; Eimer, Kiss, Press, & Sauter, 2009; Kiss, Grubert, Petersen, & Eimer, 2012; Kiss & Eimer, 2011; Lamy & Zoaris, 2009; Liao & Yeh, 2011; Lien, Ruthruff, & Cornett, 2010; Lu & Han, 2009). The following sections discuss

the main theoretical accounts of IF interference, presenting evidence for and against bottom-up and top-down attentional selection.

1.6.3. Automatic capture account

Theeuwes (1992) presented participants with a diamond-shaped target surrounded by circular distractors. Participants were asked to respond to the orientation of a line segment embedded within the odd-shaped target. When one of the distractors was also a different colour (a colour IF) attention was captured by the IF and RTs increased. This pattern of effects was present even though the identity of the target (diamond shape) remained the same throughout the experiment and despite the IF never coinciding with the target (i.e. an additional singleton paradigm). Thus, top-down knowledge of the target identity was unable to prevent attentional capture by the IF. Furthermore, this attentional capture only occurred when the colour IF was more salient than the target: a bright red IF amongst green items showed interference but a light-green IF amongst mid-green items did not. Theeuwes argued that this was clear evidence for stimulus-driven attentional capture that is guided by the salience of the search items.

Theeuwes work generated much interest in bottom-up attentional capture and, more specifically, the role of salience. The idea of a salience map is central to many theories of visual search (e.g. Cave & Wolfe, 1990; Itti & Koch, 2001; Wolfe, 1994) with its main role being to sum incoming contrast signals and direct attention to the most salient spatial location of a scene. Recently, the observation that less salient items cannot capture attention has been questioned by Zehetleitner, Koch, Goschy, and Müller (2013). They argue that inherent noise within the salience map (e.g. Humphreys & Müller, 1993; Wolfe, 1994; Wolfe et al., 1989) means salience computations are a stochastic process – the salience signals form probability distributions around competing stimuli. The nature of the distributions means that they are

able to overlap. Where this overlap occurs there is a chance that the competing IF will capture attention, even if this IF is less salient. Particularly relevant here is that Zehetleitner et al.'s (2013) theory suggests a dynamic ongoing competition for selection. They argue that the noisy saliency computations occur in parallel at the spatial locations of the search items. When enough evidence has accumulated for a stimulus it reaches a decision threshold and is selected for attention. This is clearly analogous to the dynamic target selection process at the heart of the CRT. In fact, it extends Song and Nakayama's (2008) theory of dynamic competition underlying target selection and provides a theoretical basis for how a distractor may be initially selected as the movement target both under normal circumstances (i.e. without an IF) and when an IF is present.

1.6.4 Top-down search modes

The first challenge to Theeuwes (1992) theory came from the contingent-capture account (Folk, Remington, & Johnston, 1992). This states that an observer is able to engage a particular attentional set depending on the target-defining feature. Any item outside of this set should be ignored, hence an IF defined along a different dimension should fail to capture attention. Clearly Folk et al.'s (1992) contingent-capture hypothesis is in direct opposition to Theeuwes (1992) attentional capture theory. The following discussion focuses on two more top-down theories that question Theeuwes (1992) account.

Bacon and Egeth (1994) argued that top-down mechanisms were able to select from two distinct search modes depending on the framing of the task. Observers may enter singleton detection mode or feature search mode. Singleton detection mode selects unique items from the search array based on their bottom-up salience. Thus it is implemented in search tasks where the target is not pre-defined. If, for example, a participant does not know

what colour the target will be (although they do know the target is defined along the colour dimension) singleton detection will choose the odd item. In search tasks with one target surrounded by homogenous distractors this search mode is successful since the only 'different' item on the screen is the search target. However, when a distractor is also a singleton (e.g. the red circle in Theeuwes (1992)) singleton detection mode may lead to IF selection (see Burra & Kerzel, 2013; for recent evidence). Bacon and Egeth (1994) showed that had Theeuwes (1992) participants been using feature search mode – deliberately searching for the green diamond – the IF would not have interfered with performance. Rather than presenting only one odd-shaped target item Bacon and Egeth (1994) added extra shapes to the display. Thus, the target was still the diamond but observers could not simply rely on the uniqueness of the shape versus the other distractors to select the target. Instead they had to engage feature search mode whereby they direct their attention exclusively to the target-defining feature. Under these conditions the colour IF no longer captured attention.

Neurophysiological evidence also highlights the importance of target certainty on IF interference. Of particular interest are ERP studies focusing on the N2pc component. The N2pc component is recognised as a marker of attentional selection (e.g. Hickey, McDonald, & Theeuwes, 2006; Luck & Hillyard, 1994; Luck, Woodman, & Vogel, 2000) referring to negativity in posterior electrodes contralateral to an attended stimulus. When searching for an ambiguous target (i.e. the observer knows the target is an odd-shaped item but does not know whether it will be a circle or square from trial-to-trial) the presence of an IF produces an N2pc component. However, when the target was unambiguous (i.e. the observer knew the target was a circle) no N2pc was elicited (Akyürek & Schubö, 2011). Furthermore, Eimer and Kiss (2010) showed that when participants were forced to engage singleton detection mode by using two possible target colours an IF produced both behavioural and N2pc capture effects.

No such effects were observed in feature search mode (one target colour). This research supports Bacon and Egeth's (1994) conclusion that attentional capture is modulated by top-down guidance inferred by the search mode employed. If singleton-detection mode is engaged then the IF is able to capture attention (see, Eimer et al., 2009; and Lien et al., 2010; for similar evidence).

The top-down versus bottom-up debate has continued, with arguments and counter-arguments for and against top-down modulation of bottom-up attentional capture (for instance, see Theeuwes, 2004; and, Leber & Egeth, 2006). Indeed, yet another account of IF interference, the dimension-weighting account (DWA) suggests that even in singleton detection mode the selection decision is still under some top-down guidance (Müller, Heller, & Ziegler, 1995; Müller, Reimann, & Krummenacher, 2003).

1.6.5 Dimension-weighting account

DWA argues that there is a finite weight that can be spread across all dimensions of a search array. As one dimension repeatedly signals the target the weight attached to that dimension increases and the weight attached to other irrelevant dimensions decreases accordingly. Experiments that manipulate the predictability of the IF offer support to DWA. For instance, Geyer, Müller and Krummenacher (2008) presented participants with displays similar to those used by Theeuwes (1992). Geyer et al. (2008) showed that when the IF singleton was present on just 20% of trials there was a far greater effect on RTs and eye-movement latencies than when the IF singleton was present on 50% or 80% of trials. Similarly, Müller, Geyer, Zehetleitner, and Krummenacher (2009) showed that the presence of a colour IF in an orientation search task interfered with performance, but that this interference reduced as the proportion of IF present trials increased from 20% to 50% to 80%. These results show that the

attentional system requires sufficient incentive to shift the weight towards one dimension over another. In the 20% conditions the incentive to suppress the colour IF is low because it rarely appears and hence it captures attention more readily on the trials that it does occur. Importantly, the target identity remained the same throughout these experiments. Hence, the weight attached to the target/IF dimensions was taken into account even in feature search mode, allowing capture to occur with rare IFs. These findings are inconsistent with Bacon and Egeth (1994) who stated that feature search mode should be impenetrable to attentional capture regardless of the predictability of the IF (see Noesen, Lien, & Ruthruff, 2014; for evidence that feature search mode overcomes capture from rare IFs).

1.6.6 Outlook

As shown by the discussion above there is little agreement between proponents of automatic attentional capture and those arguing for top-down attentional control. In short, there are two main ways by which top-down control can modulate IF interference. Firstly, the predictability of the target feature determines which of Bacon & Egeth's (1994) attentional modes is selected. If the feature is unpredictable the observer must rely on singleton detection mode which is vulnerable to IF interference. Secondly, predictability of the IF presence alters the dimensional weight attached to the search dimensions (e.g. Müller et al., 1995, 2003) with a frequently occurring IF being easily suppressed (e.g. Geyer et al., 2008). Chapter 5 will examine the interaction of these two top-down factors. The majority of recent research into search mode modulation of IF interference has used ERPs as a marker of attentional capture (e.g. Ansorge et al, 2011; Eimer et al., 2009; Kiss et al., 2012; Kiss & Eimer, 2011; Lien et al., 2010). The studies in Chapter 5 will attempt to demonstrate the effects of search mode and IF predictability using the CRT.

By using the CRT we will also attempt to separate bottom-up and top-down biases contributing to IF interference. It has been suggested that stimulus-driven attentional capture always precedes top-down control (see Theeuwes (2010) for review; Egeth, Leonard, & Leber (2010) for commentary; and Theeuwes, 2010b for response). Theeuwes (2010) stated that the initial sweep through the visual system is entirely stimulus-driven and top-down control only exerts an influence via later feedback mechanisms (see Hochstein & Ahissar, 2002; for a consistent theoretical framework). Hence, top-down control is never fully 'in charge' of visual attention from the outset – bottom-up input influences transfer from preattentive to attentive processing with top-down modulation occurring after this transfer. If this is truly the case then by using the CRT we may be able to dissociate stimulus-driven and goal-directed influences on IF interference. IL could index salience-based capture and be modulated by the IF regardless of its predictability, whilst MD could be unaffected by the IF since by that point it would be suppressed by top-down input.

1.7 Irrelevant feature coincidence with multiple search items

Whilst Chapter 5 aims to examine the bottom-up and top-down processes underlying attentional capture, Chapter 6 focuses on the effects of an IF coinciding with multiple search items. Specifically, Chapter 6 will investigate whether allowing the IF to coincide with multiple search items can also facilitate search. This may seem an unlikely proposal given the disruption caused by the IF coinciding with one item (e.g. Theeuwes, 1992). To understand how an IF coinciding with two items may guide search we must consider Gestalt laws of grouping.

1.7.1 Proximity grouping

Almost a century ago Wertheimer (1923) first proposed what we now know as the principles of Gestalt grouping. One of the original principles stated that objects are perceived as belonging together based on their proximity: the closer they are the more likely they are to be segmented from the rest of the scene. In relation to the present discussion, on trials where a size IF coincides with both distractors in a 3-item array the distance between those items is reduced. Hence they should be grouped together. According to Duncan and Humphreys (1989) this should lead to a linkage of the weight attached to each distractor making them easier to suppress. In this way the two IF items have facilitated rather than disrupted search. The experiments in Chapter 6 will present participants with a factorial combination of IF trials creating an equal chance that the target will be large or small and the distractors will be both small, both large, or of different sizes. Because the IF presence/coincidence and the target colour will be unpredictable it opens up the possibility that bottom-up grouping mechanisms will influence search.

1.7.2 Similarity grouping

As well as proximity grouping the presence of the IF could also promote similarity grouping. Hence, items of the same size may be segmented from the other search item. Whereas the potential effects of proximity grouping are positive (i.e. improved performance at Dd and DD versus baseline performance at dd) the effects of similarity grouping are negative. Here, performance would be disrupted when the distractor sizes are unequal (Dd) compared to the baseline condition (dd). Furthermore, the two mechanisms of grouping may be in conflict or agreement with one another. For instance, when the target is small but the two distractors are large the distractors are grouped according to both proximity and size similarity. This should result in efficient target selection. However, when the search array comprises a large target,

one large distractor, and one small distractor the two distractors are grouped by neither proximity nor similarity. In fact, the target item is grouped by similarity and proximity with one distractor. In this condition search should be disrupted by grouping promoted by the coincidence of the IF with two items.

1.7.3 Time course of proximity and similarity grouping

If the experiments in Chapter 6 are able to demonstrate proximity and similarity grouping it may also be possible to use the CRT to separate them in time. Song and Nakayama (2006) demonstrated the sensitivity of the CRT to grouping influences (see 1.3.1.2) but did not attempt to map distinct grouping processes onto IL and MD.

Research has shown that proximity grouping occurs faster than grouping by similarity (e.g. Ben-Av & Sagi, 1995; Han & Humphreys, 1999; Han, Humphreys, & Chen, 1999). For instance, Han et al. (1999) presented participants with circles that made up a global letter (H/E). The percept of the global letter was promoted by grouping of the circles by proximity, similarity, or uniform connectedness (see Palmer & Rock, 1994). RTs to discriminate the identity of the global letter were faster when the circles grouped according to proximity versus similarity (uniform connectedness only exerted effects when combined with similarity grouping). Furthermore, investigations using ERP recordings have shown that proximity grouping modulates both early activity in medial occipital regions and late activity in occipito-parietal cortex, whereas similarity grouping by colour (Han, Ding, & Song, 2002) or shape (Han, Song, Ding, Yund, & Woods, 2001) modulates only late occipito-temporal activity (see also Han, 2004). In relation to the present studies, if proximity and similarity grouping influence target selection at different time points we may be able to map these

grouping processes onto the two reach parameters, in a manner similar to that predicted for global and local processing in Chapter 4.

1.8 Outline of thesis

The current body of work will use the CRT to shed light on the dynamic processing underlying target selection. Firstly, we attempt to build on the current understanding of the CRT by examining the initial direction of trajectory deviation and by increasing the number of outcome measures (Chapter 2). After replicating Song and Nakayama's (2006) findings we will use the implicit predictive nature of the PoP methodology to probe the role of the motor system in generating predictions (Chapter 3). Chapter 4 then moves away from the colour PoP design to examine whether the CRT is able to reflect global-to-local processing of the visual scene. Finally, Chapters 5 and 6 examine the effects of IFs on target selection, particularly focusing on the impact of top-down factors such as target/IF predictability and whether an IF coinciding with multiple search items promotes grouping and is able to facilitate search. The thesis concludes with a discussion of the empirical findings highlighting the added insight provided by the CRT.

CHAPTER 2

The Effects of Distracting Items on Target Localisation

2.0.1 Abstract

The common thread running through this thesis is the choice reaching task (CRT) employed to investigate attentional processing. Typically, the participant is presented with three items and asked to reach and touch the feature target (i.e. the 'odd-one-out'). Insight into the target selection decision is gained from the kinematics of the movement: the initiation latency (IL), movement duration, total time, and maximum deviation of the reach trajectory (MD). The present chapter set out to investigate whether further movement parameters (e.g. peak velocity variables) could provide added insight into the selection process, whilst also examining the existing parameters more closely. In general, peak velocity variables did not add to our understanding of target selection although including velocity peaks as a factor did produce a total time cost, in contrast to a curved versus straight distinction. An examination of the initial direction of reach trajectories was also conducted in Experiment 2.1. The majority of reaches were initiated towards the target or in between the target and distractors. This suggests that the target had achieved the activation threshold prior to movement onset, or that no item had achieved the threshold and the reach was directed towards the region of highest activation. Curved trials were often directed towards the distractor. Together these results provide evidence for the dynamic competition underlying the CRT. The present chapter also replicates the key findings of Song and Nakayama (2006, 2007, 2008), including the effects of priming of pop-out in Experiment 2.2, thereby validating our paradigm prior to extending their work in the subsequent chapters.

2.0.2 Introduction

The development of the CRT for examining search performance is a relatively recent one (e.g. Song & Nakayama, 2006, 2007, 2008). The present chapter aims to build on the initial

foundations by examining more closely the existing outcome measures of the CRT and extending these measures to incorporate other kinematic markers. We also aim to replicate key results from Song and Nakayama's work in order to validate our paradigm.

Song and Nakayama examined two main indices of attentional selection: the timing of the reach and the maximum deviation of the reach trajectory from its ideal path (MD). The timing measures can be broken into two components, initiation latency (IL) and movement duration, which combine to form a total time measure. Between them these movement parameters offer insight into early and late selection processes. For instance, the IL is thought to reflect our initial selection decision whilst MD reflects the accuracy of this initial decision. If selection is successful then the reach proceeds in a straight path to the target. However, if selection is unsuccessful the trajectory requires correction mid-flight resulting in higher MD. As the following sections will show these reach parameters have enabled insight into target selection over and above that gained from using reaction times (RTs) as an index of attentional processing. This chapter goes on to examine whether additional reach variables are able to shed even greater light on the selection process.

For example, besides timing and trajectory deviation we will investigate whether peak velocity variables provide any added insight, as well as the time at which peak velocity and MD occur. Song and Nakayama (2008) showed that the parallel planning of initial incorrect and subsequent corrective movements means that the correction (i.e. MD) occurs early after reach onset (approximately 125ms; see 1.3.1.3). We will examine whether the time of MD varies according to the demands of the task or the characteristics of the movement (i.e. curvature and number of velocity peaks). That ongoing attentional selection/competition is able to influence early reach parameters is consistent with recent models of reaching that incorporate 'online-online' control allowing for early and ongoing correction of the

movement (e.g. Elliott, Hansen, Grierson, Lyons, Bennett, & Hayes, 2010). This is in contrast to traditional two-component theories that allow for online control only after an initial ballistic phase (Keele, 1968; Woodworth, 1899). Thus, as demonstrated by Song and Nakayama (2008), the influence of attentional processes on reach variables should be visible from the start to the end of the movement.

2.0.3 The present studies

Experiment 2.1 will present participants with randomly intermixed odd-colour search trials (OC) and single target trials (ST), replicating the design of Song and Nakayama (2007). The effects of display type will be examined as well as the characteristics of atypical reaches (i.e. curved reaches and reaches with multiple velocity peaks). Importantly, the outcome measures will be extended to include peak velocity measures as well as the time of peak velocity and MD. Finally, Experiment 2.1 will analyse more closely the initial direction of reach trajectories to OC targets with the aim of providing insight into the dynamic competition for attention underlying the choice reaching task (CRT; see 2.1.1).

Experiment 2.2 will investigate the effects of priming of pop-out (PoP) on the reach parameters noted above. We expect to replicate the seminal results of Song and Nakayama (2006, 2008), and in doing so, validate our own choice reaching paradigm.

Experiment 2.1: The Effect of Distracting Items and the Characteristics of Atypical Reaches

2.1.1 Introduction

Song and Nakayama (2007) showed that when single target (ST) and odd-colour (OC) search trials are randomly intermixed there was no difference in initiation latency (IL) between ST and OC trials. Their 'visuomotor hypothesis' argued that the threshold for commencing the movement is homogenised in between the levels of the 'easy' (the ST trial) and 'hard' decision (the OC trial) and cannot be adjusted on a trial-to-trial basis. Thus, there is no difference in IL. However, OC trials do show greater trajectory deviation from the ideal path. This suggests that on OC trials target selection is not complete at the time the initiation threshold is reached. Consequently there is scope for the distractors to capture attention and divert the hand path away from the target. We expect to replicate these results in the present experiment. We also aim to build on these results. For instance, does reaching to an OC item also affect the velocity of the movement? If so, are peak velocity and the number of velocity peaks informative measures of search performance that have so far been overlooked? One might predict ST reaches to show higher peak velocity for the same reason that they show lower deviation – with no distractors present the ease of achieving the target may produce faster as well as straighter movements.

This experiment will also investigate whether the time at which MD and peak velocity occur are influenced by the display type (ST vs. OC), reach trajectory (straight vs. curved), or the number of velocity peaks. As noted above, Song and Nakayama (2008) showed that the parallel planning of initial incorrect and subsequent corrective movements means that the correction occurs early after reach onset. The onset of the corrective movement should coincide with the point of maximum deviation and the first velocity peak as the reach changes trajectory. Thus, in curved trajectories where early movement correction was required the MD and first velocity peak should occur earlier than in straight trajectories where no correction was required. Experiment 2.1 will test this prediction.

When ILs are short there is a greater chance that an item other than the target has achieved the threshold for selection (Song & Nakayama, 2008). Thus there is a close relationship between IL and MD: the shorter the latency the more curved the trajectory. This also explains why curved trials show no overall time cost compared to straight trials: the inevitable increase in movement duration is offset by the shorter latency. As well as separating reaches based on trajectory curvature, Experiment 2.1 will investigate the characteristics of reaches with one versus multiple velocity peaks. Typically, goal-directed reaches show a bell-shaped velocity profile with a single velocity peak approximately halfway through the movement (e.g. Flash & Hogan, 1985). The presence of more than one peak indicates re-organisation of the movement was required to achieve the target (e.g. Paulignan, MacKenzie, Marteniuk, Jeannerod, 1991; Roy, Paulignan, Farne, Jouffrais, Boussaoud, 2000). Since both MD and the number of velocity peaks are indexing target re-selection we might expect a similar pattern of results for trials showing increased curvature and trials showing multiple velocity peaks. It will be interesting to observe whether separating trials according to a discrete measure of target selection (number of velocity peaks) produces comparable results to a separation based on maximum deviation.

Perhaps the most important research question of Experiment 2.1 concerns the deviation of the reach when presented with an OC search array. When focal attention is drawn to a distracting item the reach trajectory deviates away from the ideal path (e.g. Song & Nakayama, 2006). What is as yet unknown is exactly where the reach deviates towards. There are two possibilities derived from the notion of dynamic competition that underlies the CRT. Firstly, if the distractor erroneously achieves the activation threshold prior to movement onset the reach should be aimed directly towards that distractor, as though the item was in fact the target. Only later should the reach be corrected whereby it is diverted from the 'channel'

aligned with the distractor towards the target item. Secondly, the reach movement may be initiated before any one search item has achieved the selection threshold (especially because of the time constraints imposed in the current design; see 2.1.2). As a result the reach may initially be directed towards the region displaying the highest activation. Importantly, this region could be intermediate between two search items, with the exact trajectory determined by the relative activation achieved by the two items. This would be consistent with eye-movement studies that find saccades directed towards the "centre of gravity" of activation between search items (e.g. Findlay, 1982; He & Kowler, 1989). Of course, if selection is successful the target achieves the activation threshold and a straight reach is executed to the odd-colour target. To test these hypotheses we will compare the number of trials that fall into channels across the search array when reaching to a centrally-located OC target (Fig. 2.2). We will examine whether there are more OC reaches in the distractor channels (i.e. direct to the left or right distractor) or in the intermediate channels (i.e. between the central target and left/right distractor). More reaches in the distractor channels would suggest that direct reaches are being made to the distractor as a result of erroneous selection. More reaches in the intermediate channels would suggest that the competition is still ongoing but the trajectory is being 'pulled' in the direction of the highest activation. We will then observe the initial reach direction of curved trajectories. Those reaches with the highest curvature are presumably those where the distractor has achieved activation and, thus, we expect trajectories to be aligned with the distractor channel from the onset of the movement.

2.1.2 Method

Participants. Ten participants (one male) aged 18-33 (mean 20.5) were recruited from the student population at the University of Birmingham. All were right-handed with normal

colour vision and normal or corrected-to-normal visual acuity. Written informed consent was gained prior to participation with procedures approved by the local ethics committee.

Stimuli. Stimuli created using Psychophysics Toolbox for Matlab (Brainard, 1997) were presented on a vertical Samsung SyncMaster 940N LCD monitor (19", 1280 x 1024). OC displays consisted of three squares (3.8°x3.8°) positioned at 12, 4, and 8 o'clock around a circle (radius of 12.2°) against a black background. Two of the squares (the distractors) were green (u'=0.11, v'=0.24, L=64.43) and the other square (the target) was red (u'=0.46, v'=1.03, L=22.43) or vice versa (Fig. 2.1A). ST displays consisted of one red or green square positioned at any of the three possible target locations (Fig. 2.1B). A white fixation cross (0.9°) was presented in the centre of the screen prior to and during each trial.

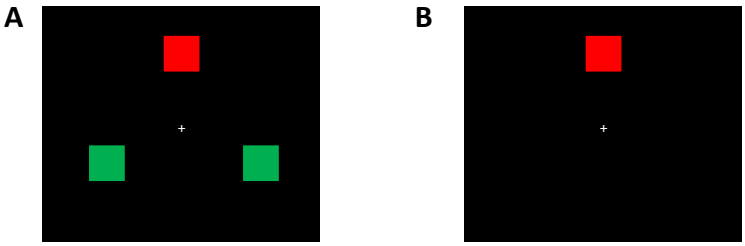

Fig. 2.1 Examples of odd-colour (OC; A) and single target (ST; B) display types.

Procedure. Participants were seated in a semi-darkened room facing a visual display. Their right hand rested beside a small, white trigger switch (aligned with body midline; 10cm from participant, 45cm from display). When prompted by on-screen instructions participants held down the trigger switch to commence each trial. A 1000ms fixation period was presented prior to the stimuli. Four sets of 96 trials were completed with 12 practice trials prior to the first set. Display type, target colour and target position were pseudorandomly selected on each

trial to ensure an equal mixture of OC and ST displays, red and green targets, and centre, left and right positions.

Participants were instructed to reach and touch the 'odd-one-out' on OC trials or the single square on ST trials as quickly and as accurately as possible. At 400ms post stimulus onset a warning tone was presented. Participants were instructed to commence their reach prior to hearing the tone (400ms was chosen as it approximated the average IL in unreported pilot testing). By forcing participants to start their reach earlier we hoped to capture ongoing competition between search items and, as a by-product, increase the number of curved trials for subsequent analysis.

As well as commencing the onscreen trial procedure the trigger switch also activated the motion-capture cameras (Qualisys ProReflex MCU240, 60Hz). The cameras recorded the position of a small (4mm), passive reflective marker attached to the participant's right index fingernail from the point at which the trigger switch was depressed until 3000ms had elapsed – long enough for the participant to complete their reach.

Design & analysis. Initial analysis was conducted using two 2-way ANOVAs: display type (ST vs. OC) x reach trajectory (straight vs. curved) and display type (ST vs. OC) x velocity peaks (1 vs. >1). The factors reach trajectory and velocity peaks could not be included in a 3-way analysis with display type because of empty cells resulting from a lack of curved ST reaches with >1 velocity peak. Dependent variables were *IL* (ms): the time at which the index finger exceeded 20mm/s following stimulus onset. *Movement duration* (ms): the time at which the index finger velocity dropped below 20mm/s following movement initiation. *Total time* (ms): the sum of IL and movement duration. *MD* (mm): the absolute deviation of the index finger trajectory from a straight line between the start and end of the movement. *Time of MD* (%): the time at which maximum deviation occurred as a proportion of the movement

duration. *Peak velocity* (mm/s): the absolute maximum peak velocity achieved between movement onset and offset. *Time of Peak Velocity* (%): the time at which the *first* velocity peak occurs as a proportion of the movement duration. *Number of velocity peaks*: the number of velocity peaks present from onset to offset where a peak is defined as a change in velocity of 25mm/s or greater for five consecutive movement frames (not included in analysis where velocity peaks was a factor). Results were collapsed across target colour and position (with no main effects of either on reach variables), both equally split according to display type. Significant ANOVA effects were investigated using paired-samples t-tests.

Following the method of Song and Nakayama (2008), reaches were defined as 'curved' where the MD value exceeded the participant's mean MD for ST reaches by over 1.5 standard deviations. This resulted in 22.5% of OC trials and 7.4% of ST trials being classified as curved.

To compare initial reach directions seven equal-size 'channels' were created that incorporated the entire display (left (L), distractor left (DL), middle left (ML), target (T), middle right (MR), distractor right (DR), and right (R); Fig. 2.2). The angle of each reach trajectory was computed by taking the arc cosine of its position at a threshold of 100mm from the start location (blue dotted line, Fig 2.2), and multiplying this value by the difference in polar coordinates between the 100mm threshold point and the end point of the movement. This gave a signed angle of deviation in the X dimension (left-right) that could be fitted into one of the seven channels. The percentage of trials whose movement angle fell inside each of the seven channels was then computed per participant when the target was present at the centre location. Planned comparisons were conducted on the channel percentages of interest; namely, the percentage of reaches falling into channel DL versus ML, and DR versus MR. More reaches in DL and DR would suggest the distracting item achieved the activation

threshold prior to initiation, whereas more reaches in ML and MR would suggest that no one item had yet achieved the threshold and the reach was directed towards the region with highest overall activation.

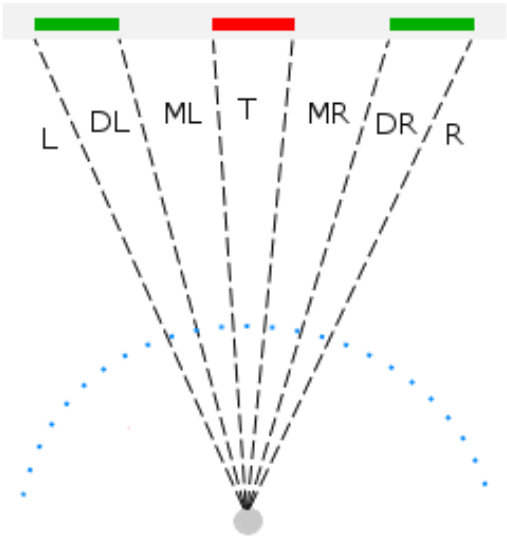

Fig. 2.2. Seven channels were created from the start point to the end point of the movement (L=Left, DL=Distractor left, ML=Middle left, T=Target, MR=Middle right, DR=Distractor right, R=Right). The percentage of trials whose movement angle fell inside each of the seven channels was then computed per participant when the OC target was presented at the centre location.

2.1.3 Results

Any error trials and outliers were removed prior to analysis. Errors included incorrect target selections (<1%), and motion-capture errors (5.8%). Following the method of Song and Nakayama (2006) outliers were defined as trials where the IL was below 100ms (i.e. anticipations) or where total time was greater than 1500ms. Mean values for each outcome measure for reaches to ST and OC displays, and for reaches exhibiting 1 or >1 velocity peaks are reported in Table 2.1.

Table 2.1. Mean reach variables (and standard deviations) for single target (ST) and odd-colour (OC) display types, and for reaches exhibiting one and more than one velocity peak.

	ST	OC	1 peak	>1peak
Initiation Latency (ms)	287 (33)	278 (35)	284 (34)	273 (32)
Movement Duration (ms)	502 (42)	512 (44)	500 (41)	562 (57)
Total Time (ms)	789 (41)	790 (46)	783 (41)	835 (68)
Maximum Deviation (mm)	41.00 (12.3)	53.25 (14.4)	43.80 (12.1)	73.47 (19.6)
Time of Maximum Deviation (%)	47.14 (5.3)	47.19 (3.9)	47.62 (4.3)	43.78 (5.4)
Peak Velocity (mm/s)	1478 (236)	1516 (264)	1534 (246)	1223 (244)
Time of Peak Velocity (%)	38.49 (4.6)	37.93 (4.8)	39.05 (4.6)	31.81 (4.9)
Number of Velocity Peaks	1.07 (0.04)	1.16 (0.05)	-	-

2.1.3.1 Display type x reach trajectory

2.1.3.1.1 Timing variables

Initiation latency. There was a main effect of display type on IL ($F(1,6)=8.96$, $p=0.024$, $\eta_p^2=0.60$). There was no difference in IL between curved and straight reaches ($p>0.250$), but a significant display type x reach trajectory interaction was observed ($F(1,6)=10.17$, $p=0.019$, $\eta_p^2=0.63$). The main effect of display type was driven by a reduction in IL on OC curved trials. As shown in Fig. 2.3, there is no difference in IL between reaches to ST and OC displays when the reach trajectory is straight ($p=0.20$). Nor is there a difference in IL on ST trials regardless of whether the reach is curved or straight ($p>0.250$). However, curved reaches to OC displays have shorter ILs than straight reaches to OC displays ($t(9)=8.07$, $p<0.001$), and there is a reduction in IL on OC curved trials compared to ST curved trials

($t(6)=3.11$, $p=0.021$; note that only 7/10 participants exhibited curved ST trials hence the differing degrees of freedom across t-tests).

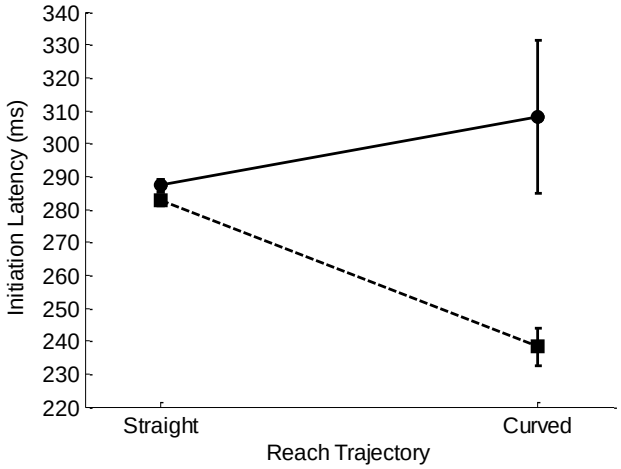

Fig. 2.3. Mean initiation latencies for single target (solid line) and odd-colour (dashed line) trials for straight and curved reach trajectories. Error bars reflect within-subjects S.E.M. (Cousineau, 2005).

Movement duration. In terms of movement duration we found main effects of both display type ($F(1,6)=9.46$, $p=0.022$, $\eta_p^2=0.61$) and reach trajectory ($F(1,6)=24.55$, $p=0.003$, $\eta_p^2=0.80$). There was also a significant interaction ($F(1,6)=10.58$, $p=0.017$, $\eta_p^2=0.64$): when the reach trajectory was straight there was no difference in movement duration between ST and OC trials (501ms vs. 503ms, $p>0.250$), when the movement was curved, however, OC reaches took significantly longer than ST reaches (610ms vs. 542ms; $t(6)=3.22$, $p=0.018$).

Total time. This increase in movement duration was offset by the shorter IL in curved OC trials and as a result, although having a slightly longer total time, there was no significant time cost for curved versus straight reaches ($p=0.054$). The pattern of timing variables for straight and curved OC trials is shown in Fig. 2.4. Total time was also unaffected by display type ($p>0.250$) and there was no display type x reach trajectory interaction ($p>0.250$).

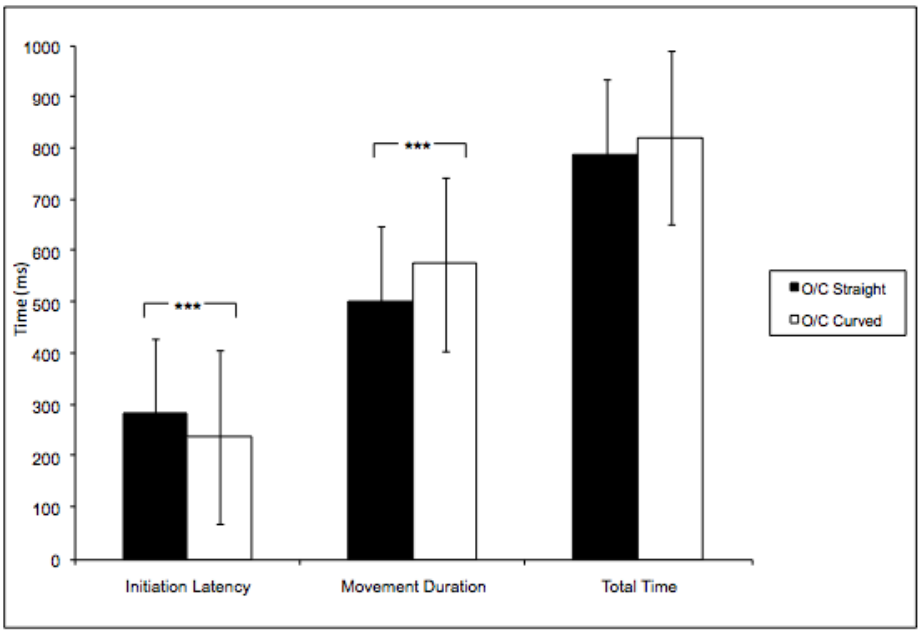

Fig. 2.4. Pattern of timing variables (initiation latency, movement duration, total time) for OC straight and OC curved reaches. Error bars show between-subjects error. ***p<0.001.

2.1.3.1.2 Maximum deviation

There was a main effect of display type on MD ($F(1,6)=7.27$, $p=0.036$, $\eta_p^2=0.55$) with reaches to ST displays showing reduced deviation compared to OC displays, as illustrated in Fig. 2.5. This is expected given the opportunity for incorrect target selection in OC but not ST trials. An effect of reach trajectory was necessarily found ($F(1,6)=75.88$, $p<0.001$, $\eta_p^2=0.93$) but no display type x reach trajectory interaction was observed ($p=0.087$). Neither factor exerted a significant effect on the time at which MD occurred, nor did they interact ($ps>0.250$).

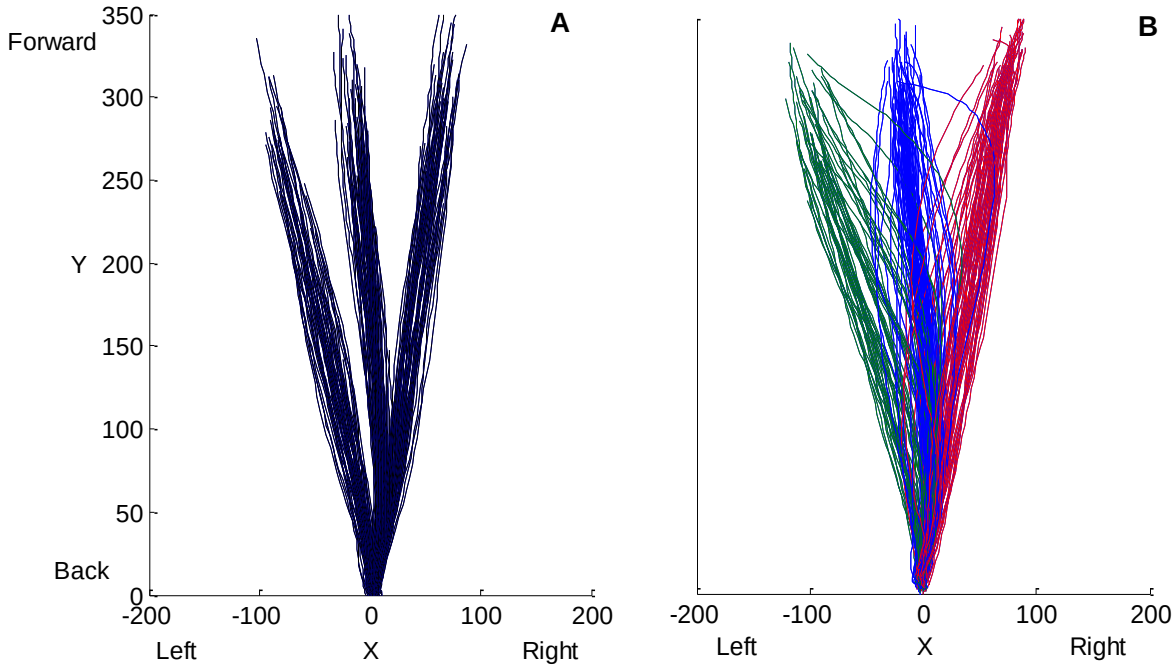

Fig. 2.5. Reach trajectories (XY coordinates; mm) from one participant for single target trials (A) and odd-colour search trials (B).

2.1.3.1.3 Peak velocity

There was no effect of display type on peak velocity (p=0.16) or the time at which it occurred (p>0.250). Peak velocity was also unaffected by reach trajectory (straight=1494mm/s, curved=1538mm/s; p=0.13) however, curved reaches did show an earlier time of peak velocity than straight reaches (F(1,6)=13.52, p=0.01, η_p^2=0.69). No interactions were observed for either peak velocity or the time of peak velocity (ps>0.250). Finally, the number of velocity peaks did not differ between ST and OC trials (p>0.250), but was affected by reach trajectory (straight=1.09, curved=1.49; F(1,6)=21.12, p=0.004, η_p^2=0.78). This reflects the target re-selection that is producing the curved reach trajectory. Fig. 2.6 separates one participant's curved velocity profiles into reaches exhibiting one and >1 velocity peak. No interaction between display type and reach trajectory was observed (p=0.08).

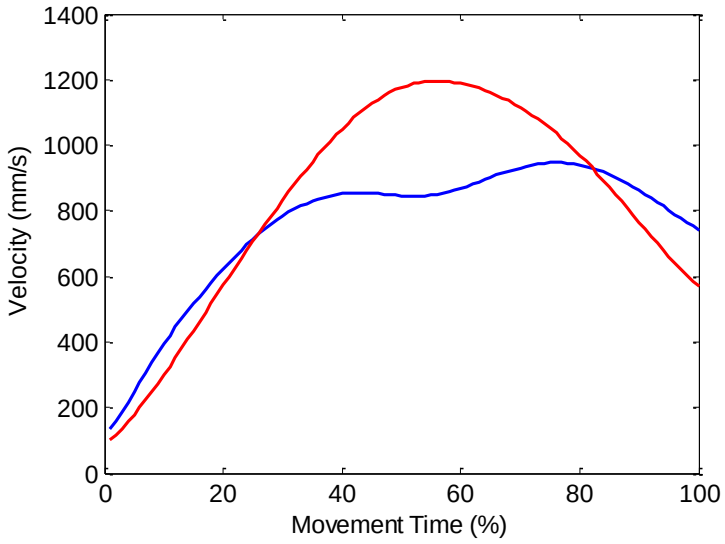

Fig. 2.6. Average normalised velocity profiles for one participant for curved reaches showing one (red) and >1 (blue) velocity peaks.

2.1.3.2 Display type x velocity peaks

For simplicity, main effects of display type are only reported if they differ to those reported in 2.1.3.1 Display type x reach trajectory.

2.1.3.2.1 Timing variables

Initiation latency. There was no main effect of velocity peaks on IL (p>0.250), but there was a significant display type x velocity peaks interaction (F(1,9)=15.15, p=0.004, η_p^2=0.63). T-tests revealed no difference in IL between ST and OC trials when the reaches had one velocity peak (286ms vs. 281ms; p>0.250). When the reaches had >1 peaks ST trials had increased ILs compared to one peak trials (286ms vs. 304ms; t(9)=2.52, p=0.033), whereas OC trials had reduced ILs in >1 peak trials compared to one peak trials (258ms vs. 281ms; t(9)=3.53, p=0.006). This interaction is analogous to that between display type and reach trajectory reported in 2.1.3.1.1.

Movement duration & total time. Unlike reach trajectory, the number of velocity peaks also affects both the movement duration ($F(1,9)=33.69$, $p<0.001$, $\eta_p^2=0.79$) and total time ($F(1,9)=20.76$, $p<0.005$, $\eta_p^2=0.70$). Here, markedly increased movement durations on >1 peak trials are not offset by shorter ILs, resulting in an overall time cost of >1 peak trials (see Fig. 2.7 for OC reaches). No interactions between display type and velocity peaks were observed for movement duration or total time (ps>0.14).

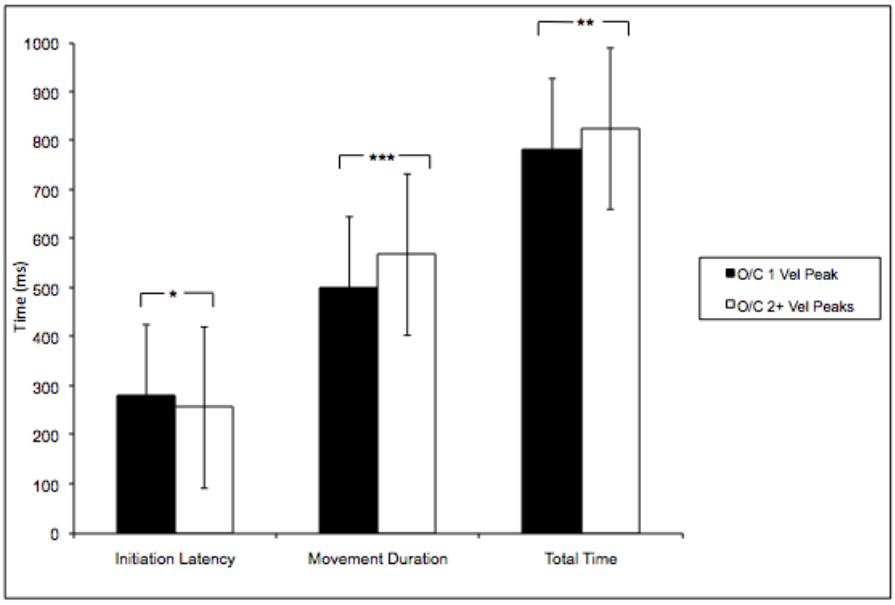

Fig. 2.7. Pattern of timing variables (initiation latency, movement duration, total time) for OC trials with one and >1 velocity peaks. Error bars show between-subjects standard error. *$p<0.05$, **$p<0.005$, ***$p<0.001$.

2.1.3.2.2 Maximum deviation

There was a main effect of velocity peaks on MD ($F(1,9)=52.33$, $p<0.001$, $\eta_p^2=0.85$), and a significant display type x velocity peaks interaction ($F(1,9)=32.73$, $p<0.001$, $\eta_p^2=0.78$). Whilst there is a moderate difference in MD between ST and OC trials when reaches have one velocity peak (40.21mm vs. 47.88mm; $t(9)=2.55$, $p=0.031$), this difference increases

markedly when the reaches have >1 peak (50.59mm vs. 83.04mm; $t(9)=6.85$, $p<0.001$). It is also worth noting that the difference in MD between OC reaches with one and >1 velocity peak (35.16mm; $t(9)=8.46$, $p<0.001$) is much larger than this difference for ST reaches (10.38mm; $t(9)=3.01$, $p<0.05$).

The time at which MD occurs is also affected by velocity peaks ($F(1,9)=14.50$, $p=0.004$, $\eta_p^2=0.62$). Trials with one peak show a later time of MD than those with more than one peak (Table 2.1). No display type x velocity peaks interaction was observed for time of MD ($p>0.250$).

2.1.3.2.3 Peak velocity

When we include velocity peaks as a factor rather than reach trajectory we see a main effect of display type on peak velocity ($F(1,9)=19.22$, $p=0.002$, $\eta_p^2=0.68$) with ST trials having lower peak velocity than OC trials (Table 2.1). Reaches with one velocity peak have higher peak velocity than those with >1 peaks ($F(1,9)=156.00$, $p<0.001$, $\eta_p^2=0.95$). There was no display type x velocity peaks interaction on peak velocity ($p=0.07$).

Finally, the time at which peak velocity occurred was influenced by display type ($F(1,9)=7.07$, $p=0.026$, $\eta_p^2=0.44$) and velocity peaks ($F(1,9)=27.14$, $p=0.001$, $\eta_p^2=0.75$). A significant display type x velocity peaks interaction ($F(1,9)=7.72$, $p=0.021$, $\eta_p^2=0.46$) showed that ST trials exhibit later peak velocity but only when the trial has >1 velocity peak (35.15% vs. 30.48%; $t(9)=2.80$, $p=0.021$).

2.1.3.3 The initial direction of reach trajectories

We tested whether on OC trials there are a higher proportion of reaches that are initiated directly towards a distractor (DL/DR) or to the region in between the target and distractor

(ML/MR; see Fig. 2.2). Results are shown in Fig. 2.8A. There were significantly more reaches initially directed towards ML than towards DL (29.1% vs. 4.6%; $t(8)=3.29$, $p<0.05$). Likewise, there are a greater percentage of reaches directed towards MR than DR (32.8% vs. 5.4%; $t(8)=4.21$, $p<0.005$). Thus, participants are more likely to direct their movement to a location intermediate between the target and a distractor than they are to reach directly toward the distractor.

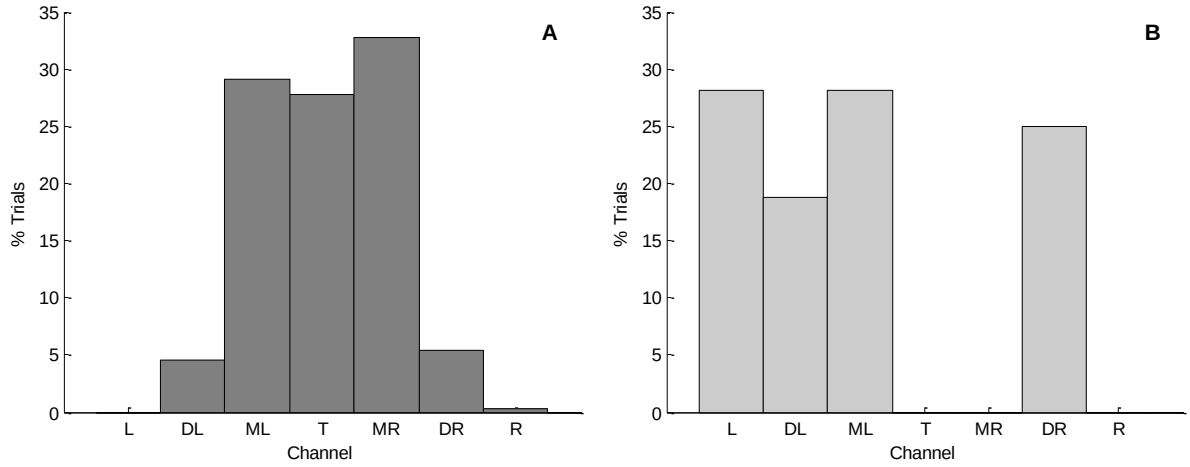

Fig. 2.8. The percentage of reach trajectories that fall within each channel 100mm after movement initiation (see Fig. 2.2). Panel A shows all odd-colour reach trajectories. Panel B shows curved odd-colour trajectories. L=Left, DL=Distractor Left, ML=Middle Left, T=Target, MR=Middle Right, DR=Distractor Right, R=Right.

We also observed whether those OC trajectories displaying greater curvature (>1.5 standard deviations from participant's mean MD in ST trials) were directed towards either the left (DL) or right distractor (DR) or towards an intermediate location (ML/MR). Results are shown in Fig. 2.8B. It is clear that there are a higher proportion of trials aligned with the distractor channels (DL=18.1%, DR=25.0%) than there are when all trials are considered

together (DL = 4.6%, DR = 5.4%; Fig. 2.8A). Note, however that the number of curved trials to the centre target represents only 15% of the original 22.5% of OC trials that were classified as curved. Hence paired-samples t-tests between DL/DR All OC trials and DL/DR Curved OC trials did not reach significance (*p*s>0.250). Nevertheless, with the caution required when inferring from a small sample size, the pattern suggests that those trajectories that are most curved represent trials where the distracting item achieves the activation threshold prior to movement initiation. Thus, the reach trajectory proceeds directly towards the distractor. When all trials are considered together it appears more likely that the target achieves activation, or that the reach is directed to a region of highest sub-threshold activation in between the target and a distractor.

2.1.4 Discussion

In the introduction (2.1.1) a series of predictions were outlined concerning the effects of display type, trajectory curvature and velocity peaks on reach parameters. Some of these predictions were based on previous findings (e.g. Song & Nakayama, 2007, 2008), whilst others were more speculative. By way of summarising the results the following discussion addresses whether they are in accordance with the stated predictions.

Song and Nakayama (2007) reported no difference in IL between ST and OC displays when they were randomly intermixed. This is because the initiation threshold is homogenised between the level of the ST and OC trials. We also demonstrated such homogenisation in the present results. For straight reaches there was no difference between ST and OC trials. However, short latencies led to increased curvature on OC trials demonstrating the cost of being unable to adjust the activation threshold on a trial-to-trial basis (Fig. 2.3).

Based on the results of Song and Nakayama (2008) we predicted no overall time cost of curved versus straight reaches. This was shown to be the case. The longer movement durations of curved trials were offset by shorter initiation latencies (Fig. 2.4). However this was not the case for reaches showing multiple velocity peaks. On these trials the movement durations were increased to such an extent that the earlier ILs were not sufficient to compensate.

In terms of MD, the presence of distracting items on the OC trials should have caused greater trajectory deviation than when no distractors were present (Song & Nakayama, 2007). This was also shown to be the case (Fig. 2.5). Likewise, MD was increased for reaches with >1 velocity peak suggesting that velocity peaks are representative of incorrect selection.

We also predicted that ST reaches would show higher peak velocity than OC reaches due to greater certainty of target selection on ST trials. In fact, there was no difference between the two display types. Reasons for the lack of effect on peak velocity are discussed in section 2.3.

Furthermore we expected peak velocity and MD to occur earlier on curved versus straight reaches. The rationale for this was that the corrective movement inherent to curved reaches occurs early after movement onset (Song & Nakayama, 2008). This corrective movement should represent the point of maximum trajectory deviation and the first velocity peak as the trajectory is re-aligned to the target path. Our results broadly supported this prediction: peak velocity did occur earlier in curved versus straight reaches and both peak velocity and MD occurred earlier on trials with >1 velocity peak.

The results presented in the final section showed that when presented with distracting items participants mostly reach either directly to the target or to a region intermediate between the target and distractors (Fig. 2.8A). This suggests that selection is either successfully

completed or is ongoing at movement initiation. On those occasions where the distractor is erroneously activated prior to reach onset the movement trajectory follows a discrete path towards the distractor (Fig. 2.8B). In general, these results support the notion of dynamic competition that forms the theoretical basis of the CRT (cf. Desimone & Duncan, 1995).

Experiment 2.1 presented a 400ms warning tone before which participants were instructed to initiate their reach. It was hoped that this would increase the number of curved reach trajectories for subsequent analysis because the selection process would still be ongoing after initiation. However, the tone did not increase the number of curved trajectories. In fact there were fewer curved trajectories to OC targets here (22.5%) than in Song and Nakayama (2008; 33%) where participants were not pressured to initiate their movement. The reason for this difference is unclear. ILs in the present experiment were between 250-350ms which is comparable to Song and Nakayama (2006, 2008). Thus, even though the warning tone did not reduce ILs, the equivalent ILs between the studies should have led to a similar proportion of curved reaches. Nevertheless, despite the low sample size the analysis of the initial direction of curved reaches still suggested that the distracting item had reached the activation threshold prior to initiation. This contrasts with when all trials are considered together where the reach was initiated towards the target or an intermediate location.

Experiment 2.2: The Effect of Priming of Pop-out on Target Selection

2.2.1 Introduction

This experiment followed the methodology of Song and Nakayama (2006). We aimed to replicate their results showing a decrease in IL, movement duration, total time, and MD across target colour repetitions (see 1.3.1.2). Such replication would demonstrate that our paradigm

was able to reveal the effects of focal attention in the same manner as Song and Nakayama's CRT and prior button-press discrimination tasks (e.g. Maljkovic & Nakayama, 1994). By the end of the colour streak we expected performance to be comparable to baseline levels where target colour remains constant (i.e. in the blocked condition). Again, we extended Song and Nakayama's (2006) results by adding peak velocity variables to the analysis.

2.2.2 Method

The methodology matched that of Experiment 2.1 with the following exceptions.

Participants. 11 participants (one male) aged 19-20 (mean 19.2) were recruited from the student population at the University of Birmingham.

Stimuli. All trials presented OC search displays (Fig. 2.1A).

Procedure. Participants completed four sets of 96 trials. Two of these sets comprised the streak condition and two comprised the blocked condition. In the streak condition target colour repetitions were embedded within the 96 trials. The length of the streaks varied between 2, 4, and 6 in one set and 3, 5, and 6 in the other. For example, in a streak of 4 the colour pattern may be 'red', 'red', 'red', 'red', 'green', where the first red and first green presentations are 'switch' trials where the colour changes after a run of repetitions. The second, third, and fourth red presentations are referred to as streak 2, streak 3, and streak 4. The positions of the different length streaks were randomised within the set of 96 trials. In the blocked condition the colour remained the same throughout the 96 trials. In one set the colour was always red, and in the other the colour was always green. Comparison of streak versus blocked performance allows us to assess the number of colour repetitions required before performance reaches baseline levels.

Design & analysis. Analysis was conducted using a 2-way ANOVA with factors streak (switch vs. 2 vs. 3 vs. 4 vs. 5 vs. 6) and target position (centre vs. right vs. left). Target position was included as a factor since a main effect of target position on reach variables was observed (see 2.2.3). Dependent variables are the same as those reported for Experiment 2.1. To test whether colour repetitions had caused outcome measures to reach baseline levels streak positions were compared against a blocked colour baseline. Bonferroni corrections were applied to paired-samples t-tests where necessary.

2.2.3 Results

A one-way ANOVA revealed no main effects of target colour on reach variables (*p*s>0.250). Target position, however, affected IL ($F(2,20)=15.66$, $p<0.001$, $\eta^2=0.61$), total time ($F(2,20)=4.92$, $p=0.018$, $\eta^2=0.33$), and MD ($F(2,20)=10.51$, $p=0.001$, $\eta^2=0.51$). Thus, target position was included as a factor with streak. This 2-way ANOVA showed no streak x target position interactions but any remaining main effects of target position are reported below. As in Experiment 2.1, error trials and outliers were removed prior to analysis (outliers: 2.8%, target selection errors: <1%, motion capture errors: 2.3%).

2.2.3.1 Timing variables

IL was reduced as the colour repeated ($F(5,50)=9.60$, $p<0.001$, $\eta_p^2=0.49$; Fig. 2.9), with significant differences between switch and streak 6 ($t(10)=4.74$, $p=0.001$), streak 2 and streak 6 ($t(10)=5.56$, $p<0.001$), and streak 3 and streak 6 ($t(10)=4.51$, $p=0.001$). Fig. 2.9 shows a steady reduction in IL over the first 5 colour repetitions, consistent with Song and Nakayama (2006), before a further significant drop from streak 5 to 6 ($t(10)=4.05$, $p=0.002$). At streak 6 IL is no different to the blocked condition ($p=0.18$; dashed line, Fig. 2.9). A main effect of

target position ($F(2,20)=13.89$, $p<0.001$ $\eta_p^2=0.58$) was observed. Both the centre (305ms) and right target positions (309ms) had shorter ILs than the left target position (320ms; $t(10)=4.71$, $p=0.001$, and $t(10)=3.85$, $p=0.003$, respectively).

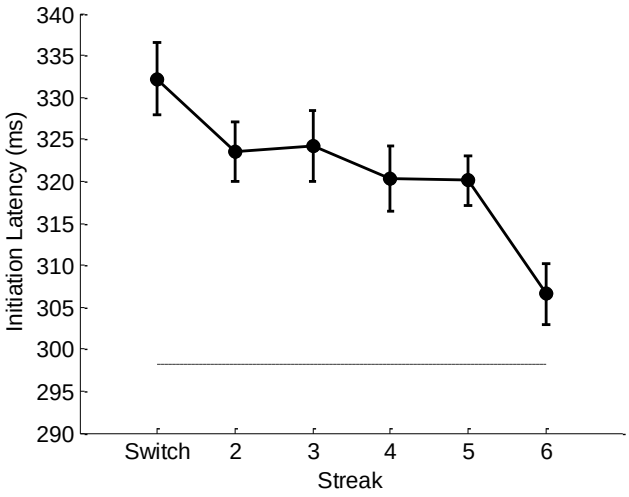

Fig. 2.9. Average initiation latency for all participants across target colour repetitions. The dashed line represents averaged baseline from blocked condition. Error bars represent within-subject standard error following the method of Cousineau (2005).

Although we also observed a significant main effect of streak on movement duration ($F(5,50)=3.35$, $p=0.011$, $\eta^2=0.25$), the pattern of reduction was more erratic than for IL. Movement duration actually showed a non-significant increase over the first few colour repetitions (from 599ms at switch to 611ms at streak 3; $p=0.08$) but subsequently decreased from streak 3 to 6 (611ms vs. 586ms; $t(10)=3.82$, $p=0.003$). Movement duration did not differ to baseline levels at any streak position (ps>0.05). There was no effect of target position on movement duration ($p=0.14$).

The combination of IL and movement duration effects produced significant main effects of streak ($F(5,50)=9.37$, $p<0.001$, $\eta_p^2=0.48$) and target position ($F(2,20)=7.29$,

p=0.004, η_p^2=0.42) on total time. Whilst being slightly less consistent than the IL streak effect (due to the movement duration pattern) there were still marked decreases, for instance, from streak 2 to streak 6 (926ms vs. 892ms; t(10)=4.58, p=0.001). Total time reached baseline levels after 6 target colour repetitions (p>0.250). The centre (898ms) and right (897ms) target positions both had significantly shorter total time than the left position (922ms; t(10)=2.69, p=0.023, and t(10)=2.72, p=0.022, respectively).

2.2.3.2 Maximum deviation

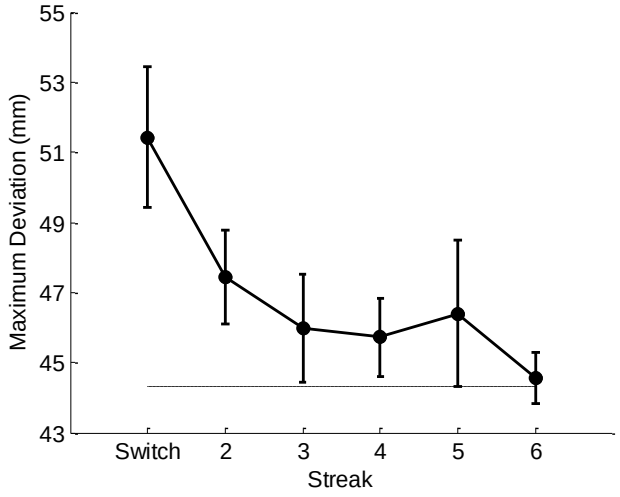

Fig. 2.10. Average maximum deviation values across target colour repetitions. The dashed line represents the averaged baseline from the blocked condition. Error bars represent within-subject standard error (Cousineau, 2005).

MD was affected by streak (F(5,50)=5.04, p=0.001, η_p^2=0.34; Fig. 2.10 and Fig. 2.11) and target position (F(2,20)=7.14, p=0.005, η_p^2=0.42). A significant reduction was observed from switch to streak 6 (t(10)=4.55, p=0.001) with borderline reductions from switch to streak 3 (t(10)=3.56, p=0.005) and streak 2 to streak 6 (t(10)=3.18, p=0.010). MD was not

significantly different to the baseline at streak 2 (p>0.250) indicating a large reduction in MD after one colour repetition. T-tests revealed the main effect of target position was caused by increased deviation at the left position (50.47mm) compared to centre (41.21mm) and right positions (45.88mm; $t(10)=4.25$, $p=0.002$, and $t(10)=2.72$, $p=0.021$, respectively).

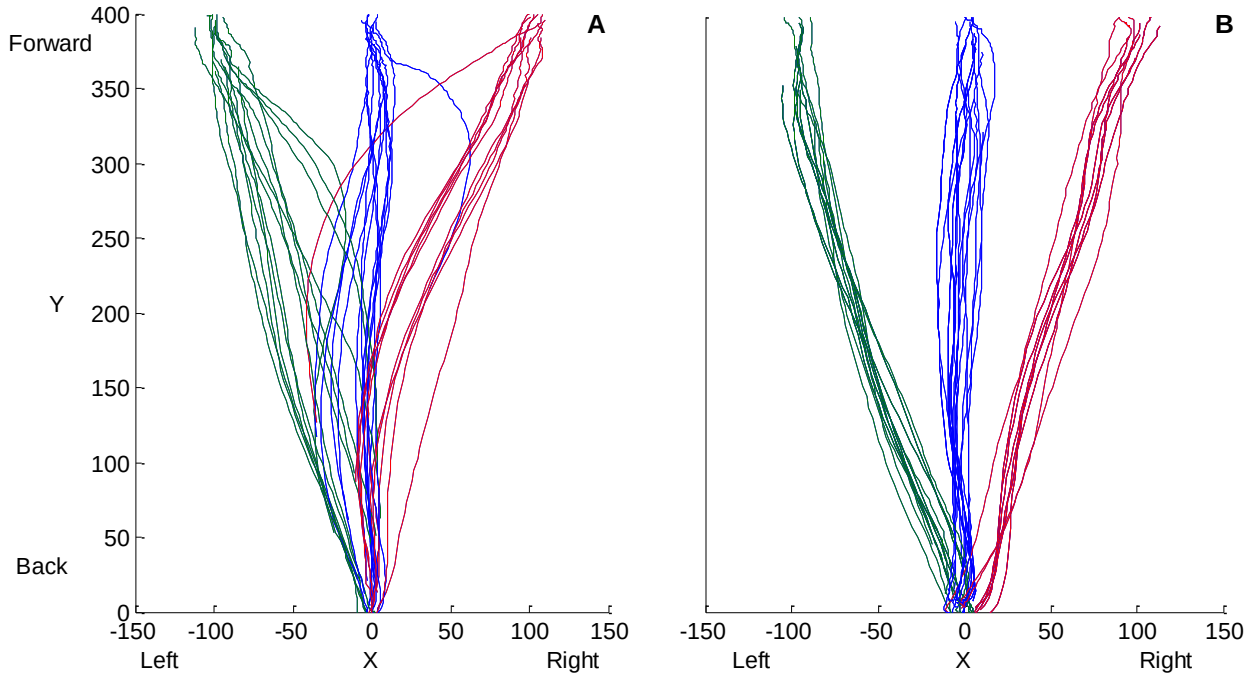

Fig. 2.11. Reach trajectories (XY coordinates; mm) for one participant on switch trial (A) and streak 6 (B) to targets at centre (blue), right (red), and left (green) positions.

There was no effect of streak on the time of MD (p>0.250), although a main effect of position was again observed ($F(2,20)=6.85$, $p=0.005$, $\eta_p^2=0.41$). MD occurred later for central targets (46.62%) than those positioned on the right (41.17%; $t(10)=3.08$, $p=0.012$) or left (40.66%; $t(10)=3.10$, $p=0.011$).

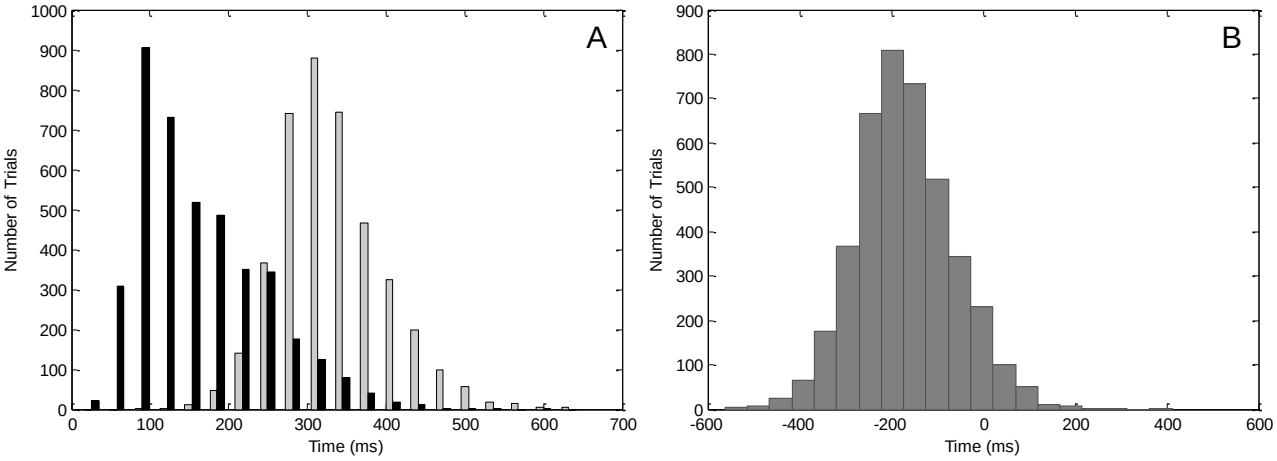

Fig. 2.12. A: Histogram showing initiation latency (grey) and time of maximum deviation values (black) pooled across participants. B: The difference in milliseconds between time of maximum deviation and initiation latency.

One of the central tenets of the CRT is that the target selection decision is the result of dynamic competition between the items in the display. This means that any corrective decision is planned in parallel to the initial incorrect decision, but reaches the activation threshold slightly later. Thus, the corrective movement (i.e. the time of MD) should occur after a shorter period of time into the reach than it took to initiate the first incorrect movement. This was shown to be the case by Song and Nakayama (2008) and is replicated here. Fig. 2.12A shows a histogram of the IL (grey) and time of MD (black) values. Evidently, MD occurs after a shorter period of the movement than it took to begin the initial movement. This is shown more clearly in Fig. 2.12B that depicts the difference between IL and time of MD values. If this histogram was centred around zero milliseconds the MD would have occurred after the same amount of time it took to initiate the reach. The fact that the histogram is shifted into negative values highlights that the initial and corrective movement

must have overlapped in their planning, and that on overage the corrective movement was planned approximately 200ms before the onset of the initial movement.

2.2.3.3 Peak velocity

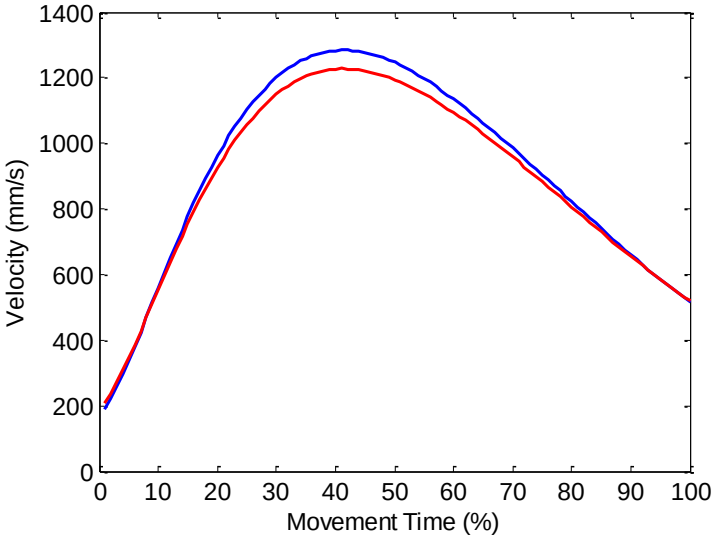

Fig. 2.13. Average normalised velocity profiles for all reaches to blocked (blue) and streak (red) targets.

The peak velocity of the reach was unaffected by streak (e.g. switch=1364mm/s, streak 6=1365mm/s; p=0.077). As shown in Fig. 2.13, when overall streak averages are compared with blocked averages there is minimal difference in peak velocity (p>0.250). There was a main effect of target position on peak velocity (F(2,20)=206.51, p<0.001, η_p^2=0.95), with the left position (1023mm/s) having a lower average velocity than both the centre (1567mm/s) and right positions (1524mm/s; t(10)=20.43, p<0.001, and t(10)=15.80, p<0.001, respectively). The time at which peak velocity occurred was unaffected by either streak or target position (ps>0.3), being constant at between 32-34% of the movement.

Finally, despite a tendency for the number of velocity peaks to decrease over target colour repetitions (from 1.18 at switch to 1.08 at streak 6), there was no main effect of streak (p>0.250). There was a main effect of target position on the number of velocity peaks ($F(2,20)=28.69$, $p<0.001$, $\eta_p^2=0.67$). Again, the left position showed poorer performance (1.29 peaks) than centre (1.03) or right positions (1.07; $t(10)=6.41$, $p<0.001$, and $t(10)=5.21$, $p<0.001$, respectively).

2.2.4 Discussion

Results showed that our choice reaching paradigm is able to index PoP biases on focal attention in the same manner as key-press target discrimination paradigms (e.g. Maljkovic & Nakayama, 1996). As target colour repeated improvements in both IL and MD were shown. There were differences in the number of colour repetitions needed for performance to reach baseline levels. For IL and total time the reduction was gradual and became more rapid towards the end of the streak. In contrast, the reduction in MD was more pronounced, after just one repetition deviation did not differ to the average value from the blocked condition.

We also showed that the planning of initial incorrect and subsequent corrective movements occurred, at least partly, in parallel. Only by using the CRT are we able to investigate this ongoing competition via examination of the reach trajectory.

2.3 General discussion

One goal of this initial chapter was to validate our choice reaching paradigm. By replicating results from the literature (Song & Nakayama, 2006, 2007, 2008) across both experiments we have achieved this aim. We also wanted to add to what we already know about the CRT. This extension of our knowledge came in two main areas – the initial direction of reaches to OC

targets, and whether the velocity of the reach offered any further insight into the selection process.

When all OC trials were considered together we observed very few reaches that were in a channel aligned with either of the distracting items. Instead, the vast majority of reaches fell in the target channel and in the intermediate channels between the target and distractors. This suggests that on the most trials target selection was either successful prior to initiation, or was still ongoing and was initially directed towards the location with the highest average activation. Interestingly, on those OC trials that exhibit the highest curvature the reaches were often directed at the left or right distractor from the outset. This indicates that there were occasions when the distractor achieved the activation threshold. When this occurred the reach needed to be corrected midflight to achieve the target. As shown in Fig. 2.13 this corrective movement is planned in parallel with the initial incorrect movement yet not early enough to prevent distractor activation.

The peak velocity of the reach or the time that it occurred gave us little extra insight into the processes of target selection in either experiment. In hindsight this is perhaps unsurprising given the fact that neither the size of the target, nor the distance to the target changed across conditions. These two variables are known to impact on the time taken to reach a target (and, therefore, the peak velocity of the movement (Fitts, 1954)), and may also explain why movement duration seemed to be less affected by display type or streak than the other movement variables.

Using the number of velocity peaks as a factor in the analysis of Experiment 2.1 did lead to some interesting findings. Longer movement durations for curved versus straight reaches were offset by shorter ILs. This was not the case for one versus >1 velocity peak trials. Whilst the >1 peak trials did start earlier, it was not early enough to offset a large

increase in movement duration. Thus, total time increased in trials with >1 peak. It seems that the trials that have multiple velocity peaks are those trials where the selection process goes most awry: when the movement needs correcting to the extent that the reorganisation necessitates an overt sub-movement (resulting in a second velocity peak). This is supported by the significant increase in MD in >1 peak trials. As a dependent variable though, the number of velocity peaks failed to add anything to what we gain from the MD measure. Being a continuous measure MD is more sensitive to smaller errors in the selection process that do not require such large-scale reorganisation as to produce another velocity peak. For this reason the remaining chapters in this thesis will focus on the IL and MD variables (although other variables will be reported where relevant). These two measures offer the clearest insight into early and ongoing selection processes. Furthermore, although there were main effects of target position on some reach parameters there were no interactions with the factors of interest. For the remaining chapters target position will be collapsed across in the same way as target colour.

CHAPTER 3

Motor Cortex Guides Selection of Predictable Movement Targets

Chapter 3 is an adapted version of Woodgate, P. J. W., Strauss, S., Sami, S., and Heinke., D. (2015). Motor Cortex Guides Selection of Predictable Movement Targets. *Behavioural Brain Research, 287,* 238-246..

3.0.1 Abstract

The previous chapter in this thesis demonstrated the sensitivity of the choice reaching task (CRT) to the colour priming of pop-out (PoP) effect. This chapter also utilises the colour PoP paradigm where streaks of same colour trials were embedded. Neuroimaging findings have shown that the motor system may be involved in predicting upcoming sensory information. If this is the case then the motor cortex should be recruited during completion of the PoP task where target colour repeats occur more frequently than chance (i.e. target colour is predictable). The present studies tested this hypothesis. Transcranial direct current stimulation (tDCS) was applied to the motor cortex whilst participants localised the odd-colour target. Where no predictability of colour was embedded reach performance was unaffected by tDCS. However, in the PoP paradigm anodal tDCS facilitated performance versus sham and cathodal tDCS. Interestingly, this improvement was apparent on maximum deviation but not initiation latency. Finally, the results of a key-press experiment suggested that motor cortex involvement is restricted to tasks where the target colour is movement-relevant. The underlying mechanism that is responsible for the effect of tDCS when reaching to a predictable target is debated (i.e. bottom-up encoding and storage versus top-down probability effects).

3.0.2 Introduction

The current chapter aims to investigate the involvement of the motor system in expectation-based guidance of target selection. More specifically, it examines whether the motor system is recruited when the defining-feature of a movement target is highly predictable (i.e. where colour repeats are more likely than chance). Positing such a role for the motor system is at odds with traditional serial stage models of the brain. These models assume that the motor

system ‘simply’ has to read out previous processing in order to execute a movement (e.g. Marr, 1980; Sternberg, 1969). Recently, however, converging evidence has implicated the motor system in cognitive operations traditionally thought to be completed ‘upstream’, consistent with the notion of a continuous, bi-directional processing pipeline (e.g. Hatsopoulos & Suminski, 2011; Resulaj, Kiani, Wolpert, & Shadlen, 2009). For instance, it has been shown that (i) learning processes in the motor system can change the psychophysical judgment of perceptual stimuli (e.g. Hecht, Vogt, Prinz, 2001; Brown, Wilson, Goodale, & Gribble, 2007; Ostry, Darainy, Mattar, Wong, & Gribble, 2010), (ii) visual discrimination is better at locations that form movement targets than elsewhere (e.g. Baldauf and Deubel, 2010; Deubel, Schneider, & Paprotta, 1998), (iii) the strength of beta oscillations in primary motor cortex varies with attention to task-relevant cues (Saleh, Reimer, Penn, Ojakangas, & Hatsopoulos, 2010), and (iv) the motor cortex accumulates perceptual evidence reflecting an individual’s expectation of the subsequent stimulus prior to executing a motor response (e.g. de Lange, Rahnev, Donner, & Lau, 2013; Donner, Siegel, Fries, & Engel, 2009).

Findings that suggest the involvement of the motor system in generating predictions/expectations are particularly relevant to the present chapter (see Schubotz, 2007; for a review). Schubotz and von Cramon (2002) asked participants to predict the size of a square based on a preceding size sequence. Analysis of fMRI activity showed that premotor cortex was activated by the attempt to predict the sequential perceptual pattern despite the lack of a movement component. Furthermore, the motor cortex has been shown to encode general uncertainty surrounding the presentation of a perceptual object based on the probability of a cue being a good predictor of a target over a trial block (Bestmann, Harrison, Blankenburg, Mars, Haggard, et al., 2008). Bestmann et al. showed that when a high

proportion of pre-cues validly predicted the target of a key-press decision motor cortex activity was higher than when pre-cues were less predictive.

The present study uses the colour priming of pop-out (PoP) methodology where target colour repetitions are embedded in trial blocks. Under such conditions predictability is high because the participant learns that over the course of a block colour repeats are more likely than switches (approximately 80:20%). Conversely, in the odd-colour (OC) versus single target (ST) design described in Chapter 2 (Experiment 2.1), predictability is low due to the unpredictability of both colour and display type. By utilising these two experimental designs, the studies in this chapter will examine the involvement of the motor system in predicting the identity of a movement target. There is a key difference between the present studies and the Bestmann et al. (2008) study in that here, the predictable feature is the movement target (i.e. reach end-point), whereas in Bestmann et al. the predictable feature signalled the effector for a key-press response. It is unclear whether Bestmann et al.'s findings will generalise to reaching movements with multiple potential targets and without an explicit pre-cue that signals the likelihood of encountering a red/green target on the upcoming trial.

Evidence that the motor cortex can form representations of perceptual information if the information is strongly related to movements (e.g. Zach, Inbar, Grinvald, Bergman, & Vaadia, 2008; Eisenberg, Shmuelof, Vaadia, & Zohary, 2011), gives additional credence to the hypothesised role of the motor system in our PoP-CRT design. For example, Zach et al. showed motor cortex neurons responded to the colour of a target when it was associated with the end point of an overt reaching movement, even when the association between colour and target had ended. It is also important to note that the present chapter is not concerned with the roles of the cerebellum (e.g. Shadmehr, Smith, & Krakauer, 2010) or the superior colliculus

(e.g. Song, Rafal, & McPeek, 2011) in movement control. Rather, it attempts to investigate the role of the motor system in expectation-based guidance of target selection.

In all studies transcranial direct current stimulation (tDCS) was applied to the motor cortex during task-completion. tDCS is known to increase (anodal tDCS) or decrease (cathodal tDCS) excitability of the underlying cortex (e.g. Nitsche & Paulus, 2001). In both cases, there are measurable behavioural consequences (e.g. Reis, Schambra, Cohen, Buch, Fritsch, et al., 2009). Although on the face of it, electrical stimulation over the motor cortex seems fairly non-specific, a recent study combining tDCS and electroencephalography demonstrated effects predominantly on the motor cortex and functionally-related areas (Notturno, Marzetti, Pizzella, Uncini, & Zappasodi, 2014).

Experiment 3.1: The Effects of tDCS on Reaching to an Unpredictable Target

3.1.1 Introduction

Experiment 3.1 followed the design of Song and Nakayama (2007; replicated in Experiment 2.1), presenting randomly intermixed ST and OC displays without colour streaks. Thus, it investigated the effects of tDCS in a CRT where predictability was low. As laid out in the introduction we did not expect a tDCS effect because research has shown the motor cortex is not recruited under such conditions (Bestmann et al., 2008). However, it is also worth noting that tDCS over the motor cortex may improve the precision of movements in general (e.g. Hummel, Heise, Celnik, Floel, Gerloff, & Cohen, 2010). Thus, Experiment 3.1 also constitutes a control experiment for Experiment 3.2 where target colour is predictable.

3.1.2 Method

Participants. 18 University of Birmingham students were recruited in exchange for cash or course credit. Participants in all 3 experiments were right-handed and had normal or corrected-to-normal colour vision. Participants were randomly assigned to an anodal (AtDCS) or sham (StDCS) stimulation group. The participant information for each group was as follows: AtDCS: n=9, 5 females, mean age 20.2, StDCS: n=9, 6 females, mean age 21.3. Procedures were approved by the local ethics committee at the University of Birmingham and informed consent was gathered from all participants after the completion of a tDCS safety screening questionnaire.

Procedure. The procedure matched that of Experiment 2.1 with the addition of the tDCS protocol. A battery-driven stimulator delivered a 1.2 mA current (NeuroConn DC-Stimulator Plus, Rogue Resolutions) to two electrodes covered by saline-soaked sponges (5cm x 5cm) to give a current density of 0.048 mA/cm^2. The anode was positioned over the left motor cortex (contralateral to right-hand), at position C3' of the 10-20 EEG system, with the reference electrode positioned above the right supraorbital ridge. Stimulation was administered for 20 minutes, ramping up and down at the start and end over 10 seconds. StDCS participants received stimulation for a brief period of 20 seconds at both the beginning and end of the trial block, with the current ramping up to 1.2mA over 10 seconds, and immediately ramping down to zero again.

Design & analysis. Participants in both stimulation conditions participated in three testing sessions: Pre-, during- and post-tDCS. Each of these sessions was divided into two blocks of 96 trials with a short break between each block. 50% of each block were ST trials and 50% were OC trials (randomly mixed) with target colour pseudorandomly assigned to ensure a 50-50 split of red and green.

Following the pre-tDCS session the tDCS equipment was set-up and stimulation activated. The 20-minute stimulation period (AtDCS) was sufficient for the participant to complete the during-tDCS session (2x96 trials). After a 30-minute break the participant completed a further 2 blocks in the post-tDCS session.

Again, the analysis focused on initiation latency (IL) and maximum deviation (MD). Firstly, a mixed ANOVA was conducted with factors stimulation (anodal vs. sham), display type (ST vs. OC), and session (pre- vs. during- vs. post-tDCS). Significant ANOVA effects were explored with paired-samples t-tests. Despite being included in the ANOVA (to provide accurate analysis of session and streak effects) we do not report the effects of stimulation. Instead, a standardised score was calculated by subtracting the pre-tDCS performance from during- and post-tDCS performance. This way any *a priori* stimulation group differences were excluded from the analysis. This standardised score was then subject to a simple effects analysis comparing AtDCS and StDCS at the during- and post-tDCS sessions.

3.1.3 Results

Data were collapsed across target colour and position (both equally split across conditions) and any outliers and error trials were removed. Outliers (2.2% of trials) were defined differently to Chapter 2 because there was no total time measure included in this and the following chapters (Chapter 2 replicated Song and Nakayama (2006) in excluding trials with total time > 1500ms). Thus outliers were classified as trials where the IL was >2 standard deviations from the mean per participant. Errors included incorrect target responses (<0.1% of trials) and technical motion capture errors (<1%).

Fig. 3.1 shows exemplar reach trajectories from a representative participant to ST and OC displays prior to receiving AtDCS. The analysis of the raw ILs revealed a main effect of

session (Fig. 3.2; $F(2,32)=34.40$, $p<0.001$, $\eta_p^2=0.68$) with pre-tDCS having longer ILs than during- ($t(17)=5.22$, $p<0.001$) and post-tDCS ($t(17)=7.27$, $p<0.001$) and post-tDCS having shorter ILs than during-tDCS ($t(17)=3.98$, $p=0.001$). The presence of this pattern in AtDCS and StDCS groups suggests it is the result of practice.

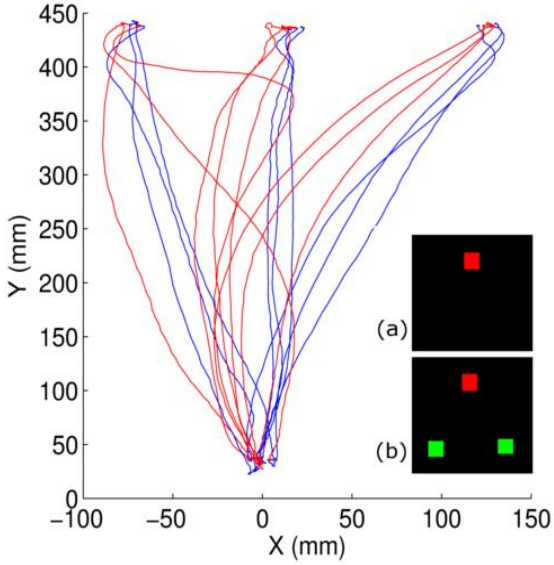

Fig. 3.1. Illustration of reach trajectories from a representative participant pre-AtDCS. Three example trajectories are shown for each target position per display type. Blue trajectories indicate reaches to single targets (see insert (a)), red trajectories to odd-colour targets (see insert (b)).

Results also replicated Song & Nakayama (2007) who found no difference in IL when the ST and OC trial types were randomly mixed (Fig. 3.2; $F(1,16)=0.17$, $p>0.250$, $\eta_p^2=0.01$). A simple effects analysis, carried out separately on during- and post-tDCS standardised ILs did not show an effect of stimulation ($F(1,16)=0.32$, $p>0.250$, $\eta^2=0.02$; and $F(1,16)=0.01$, $p>0.250$, $\eta^2<0.01$; for during- (Fig. 3.3A) and post-tDCS differences (Fig. 3.3B), respectively).

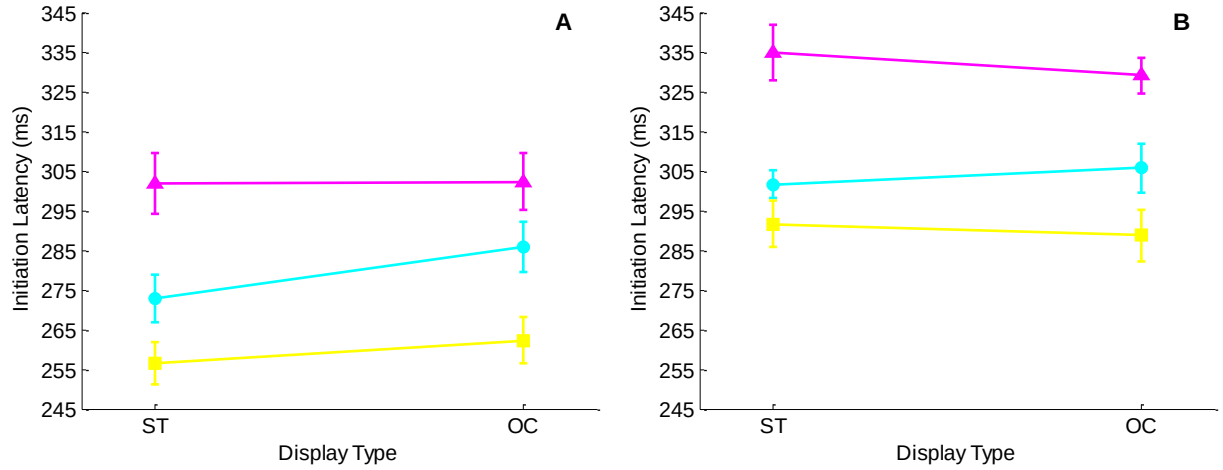

Fig. 3.2. Differences in initiation latency according to display type (ST vs. OC) and session (pre-tDCS = magenta, during-tDCS = cyan, post-tDCS = yellow) for AtDCS (A) and StDCS (B) in Experiment 3.1. Error bars reflect within-subjects standard error (Cousineau, 2005).

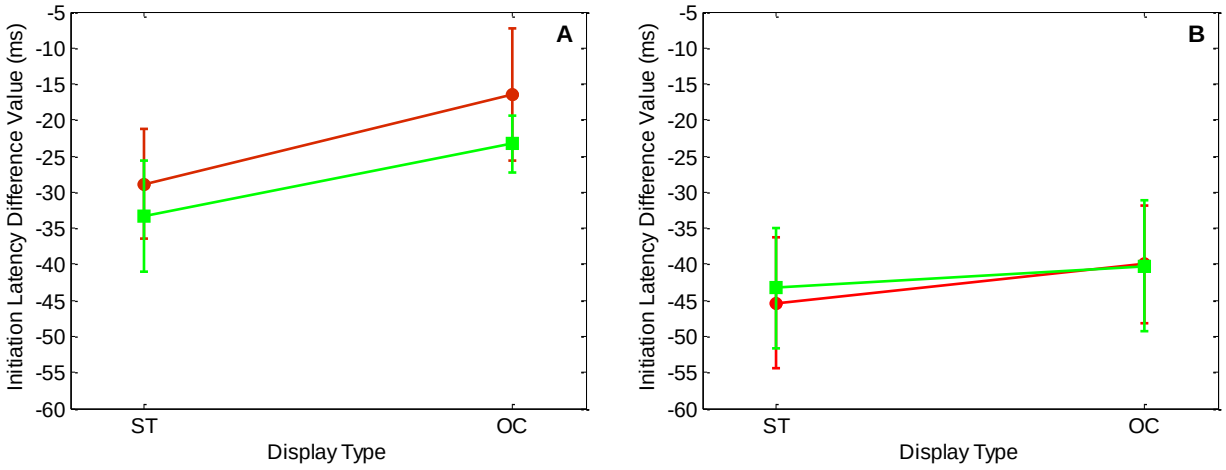

Fig. 3.3. Standardised initiation latency values for AtDCS (red) and StDCS (green) at during- (A) and post-tDCS (B). Error bars reflect between-subjects S.E.M.

The analysis of the raw MD data again showed we replicated Song & Nakayama's (2007, see also Chapter 2) findings of increased curvature for OC versus ST trials (Fig. 3.4; $F(1,16)=62.43$, $p<0.001$, $\eta_p^2=0.80$), but there was no main effect of session ($F(2,32)=0.28$, $p>0.250$, $\eta_p^2=0.02$). No interactions approached significance. Importantly, the standardised

MD scores showed no differences between stimulation groups at during- or post-tDCS (Fig 3.5A; $F(1,16)=0.32$, $p>0.250$, $\eta^2=0.02$, and, Fig. 3.5B; $F(1,16)=0.02$, $p>0.250$, $\eta^2=0.001$, respectively).

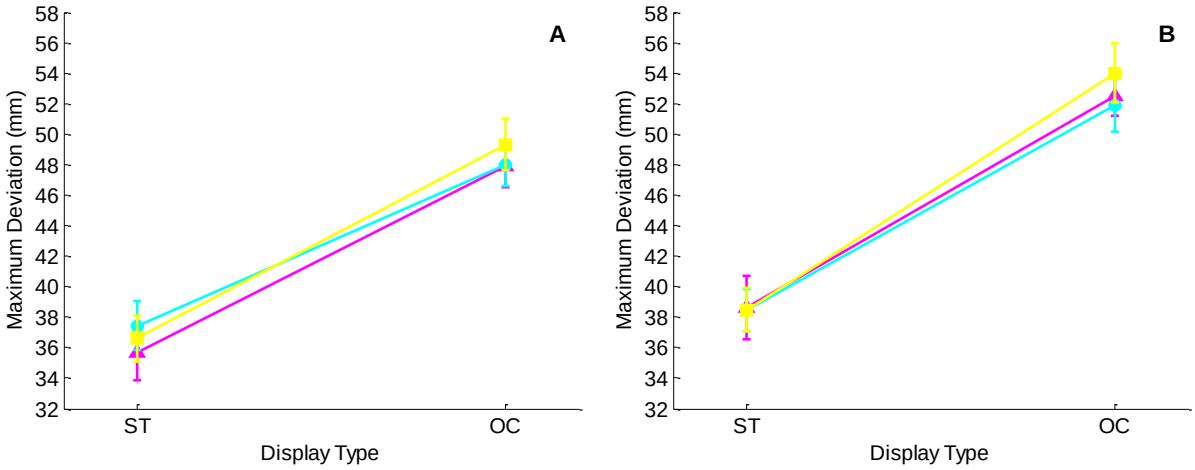

Fig. 3.4. Differences in maximum deviation according to display type (ST vs. OC) and session (pre-tDCS = magenta, during-tDCS = cyan, post-tDCS = yellow) for AtDCS (A) and StDCS (B) in Experiment 3.1. Error bars reflect within-subjects standard error (Cousineau, 2005).

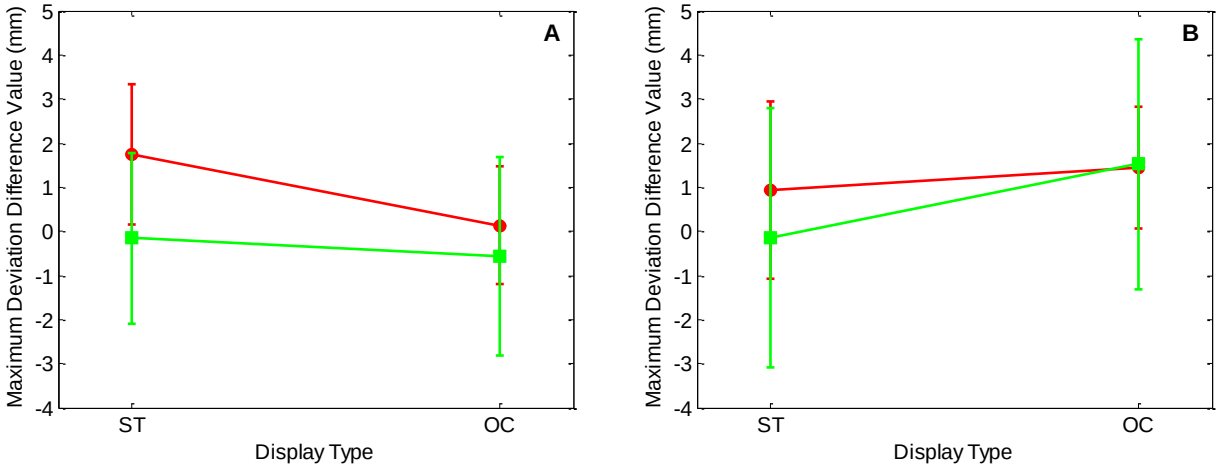

Fig. 3.5. Standardised maximum deviation values for AtDCS (red) and StDCS (green) at during- (A) and post-tDCS (B). Error bars reflect between-subjects S.E.M.

Despite the lack of systematic colour repetition the pseudorandom nature of the colour designation meant it was inevitable that some colour streaks occurred. In turn, this may have led to fluctuations in the level of target predictability across a trial block. For this reason an additional analysis was conducted whereby occurrences of consecutive OC presentations were entered into a three-way mixed ANOVA with factors stimulation (AtDCS vs. StDCS), session (pre- vs. during- vs. post-tDCS), and streak (switch vs. streak 2). Note that the streak levels were restricted to switch and streak 2 as these had equally high numbers of occurrences (43.7% of trials) whereas only 9.4% of trials were streak 3 trials. Nevertheless, PoP effects are often greatest after one repetition (e.g. Maljkovic & Nakayama, 1994) so any predictability effects should be observed from switch to streak 2. IL results remained the same as in the previous analysis with the only significant main effect being exerted by session ($F(2,32)=23.53$, $p<0.001$, $\eta_p^2=0.60$). There was no effect of streak ($p>0.250$) and, no interaction between streak and session ($p=0.24$) or stimulation ($p>0.250$). For MD, there were no effects of session ($p>0.250$) or stimulation ($p>0.250$) but a main effect of streak was observed (switch = 51.01mm, streak 2 = 47.50mm; $F(1,16)=5.54$, $p=0.032$, $\eta_p^2=0.26$). Importantly, however, there was no interaction between streak and session ($p>0.250$) or stimulation ($p>0.250$). These results suggest that, in terms of IL, ST trials disrupted any potential PoP effects when colour streaks occurred by chance. Whilst there was some PoP effect for MD the lack of interaction with session or stimulation argues against any predictability-based modulation of motor cortex involvement in this experiment.

3.1.4 Discussion

The results from Experiment 3.1 show that both reach parameters were unaffected by motor cortex stimulation. This has two important implications. Firstly, it suggests that in the absence

of any predictable colour repetition tDCS has no discernable effect on target selection. Secondly, tDCS does not lead to simple improvements in reach performance meaning that any effects in Experiment 3.2 are likely attributable to the change in predictability of the target feature.

Experiment 3.2: The Effects of tDCS on Reaching to a Predictable Target

3.2.1 Introduction

In Experiment 3.2 target colour streaks introduced statistical regularity (i.e. predictability) into the experimental design. It has been shown that the PoP effect is enhanced when the probability of a target repeat, i.e. overall predictability, is increased (see Geyer & Müller, 2009; Pascucci et al., 2012). In Experiment 1 the proportion of target colour repeats to switches is 80%:20%, hence the participant should build up an implicit expectation of a target repeat. In line with Bestmann et al.'s (2008) findings we expect the motor cortex to be recruited during the predictable PoP task. Thus the enhanced PoP effect stemming from the predictable repetition of the target should be strengthened further in the anodal stimulation group (AtDCS) but weakened in the cathodal stimulation group (CtDCS).

3.2.2 Method

The method of Experiment 3.2 replicated that of Experiment 2.2 (PoP design) with the following exceptions.

Participants. 27 University of Birmingham students were randomly assigned to either an anodal, cathodal or sham stimulation group. The participant information for each group was

as follows: AtDCS: n=9, 5 females, aged 18-29 (mean 22.1), StDCS: n=9, 5 males, aged 20-35 (mean 25.9), CtDCS: n=9, 7 females, aged 19-23 (mean 20.22).

Design & analysis. Each session (pre-, during, post-tDCS) comprised two blocks of 96 OC trials with colour streaks embedded. Again the dependent variables IL and MD were standardised by subtracting pre-tDCS performance from during- and post-tDCS for simple effects analyses between stimulation groups. Raw IL and MD values were entered into a 3-way mixed ANOVA (stimulation x session x streak) for analysis of session and streak effects. Main effects of session were investigated using paired-samples t-tests whilst planned comparisons between switch and streak 6 (based on the results reported in Chapter 2) examined the main effect of streak.

3.2.3 Results

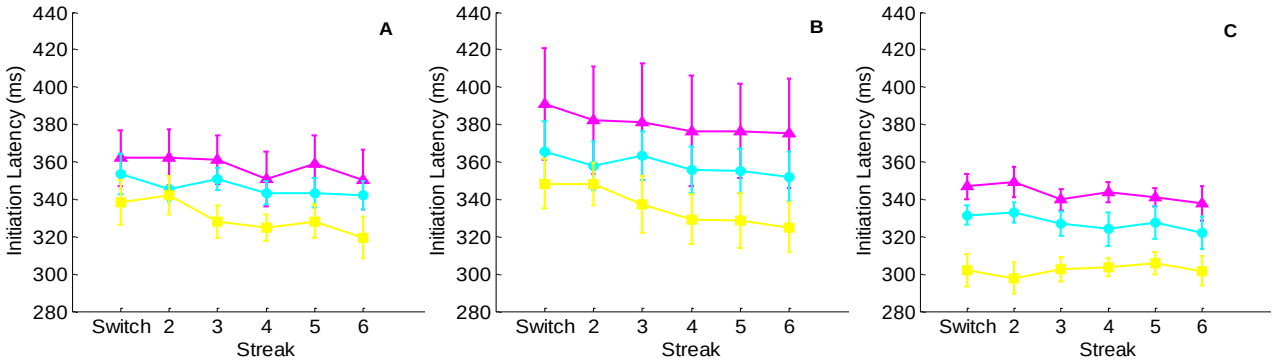

Fig. 3.6. Raw mean initiation latencies for AtDCS (A), StDCS (B), and CtDCS (C). Pre-tDCS performance is shown in magenta, during-tDCS in cyan and post-tDCS in yellow. Error bars reflect within-subjects standard error (Cousineau, 2005).

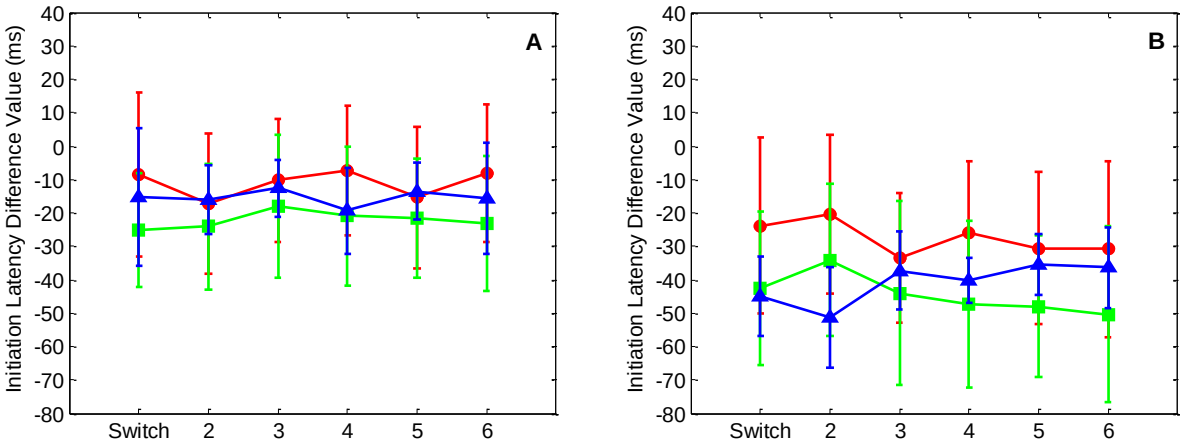

Fig. 3.7. Standardised initiation latency difference scores (red = AtDCS, green = StDCS, blue = CtDCS) for during-tDCS (A) and post-tDCS (B). Error bars reflect between-subjects S.E.M.

Data were collapsed across target colour and position (both equally split over conditions) and any outliers (1.9%) and error trials (incorrect responses: <0.1%; motion capture errors: 1.6%) were removed.

Raw IL data (Fig. 3.6) showed main effects of both session ($F(2,48)=8.33$, $p=0.001$, $\eta_p^2=0.26$) and streak ($F(5,120)=7.55$, $p<0.001$, $\eta_p^2=0.24$). As in Experiment 3.1, the main effect of session was down to practice with pre- and during-tDCS have longer ILs than post-tDCS across all stimulation groups ($t(26)=3.37$, $p=0.002$, and $t(26)=3.85$, $p=0.001$, respectively). The expected priming effect was present, as evidenced by a significant decrease from switch trial to streak 6 (344ms vs. 331ms; averaged over stimulation and session; $t(26)=4.11$, $p<0.001$). No interactions approached significance. Importantly, the standardised scores showed no effect of stimulation on IL at either during- (Fig. 3.7A; $F(2,24)=0.11$, $p=0.90$, $\eta^2=0.009$) or post-tDCS (Fig. 3.7B; $F(2,24)=0.21$, $p=0.82$, $\eta^2=0.02$).

Raw MD values (Fig. 3.8) were affected by streak ($F(5,120)=20.68$, $p<0.001$, $\eta_p^2=0.46$) and session ($F(2,48)=4.99$, $p=0.011$, $\eta_p^2=0.17$). The expected PoP pattern was present (switch = 50.70mm, streak 6 = 41.43mm; $t(26)=5.13$, $p<0.001$), and during-tDCS

showed less deviation than post-tDCS (43.30mm vs. 46.52mm; t(26)=2.35, p=0.026) when collapsed across stimulation groups. There were no significant interactions.

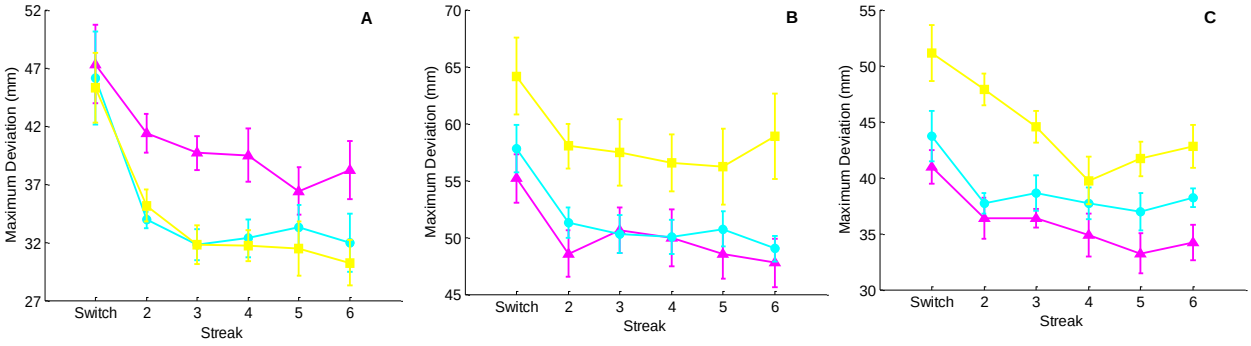

Fig. 3.8. Raw mean maximum deviation for AtDCS (A), StDCS (B), and CtDCS (C). Pre-tDCS performance is shown in magenta, during-tDCS in cyan and post-tDCS in yellow. The y-axis scale varies from figure-to-figure so that the stimulation group differences do not obscure the important differences between sessions. Error bars reflect within-subjects standard error (Cousineau, 2005).

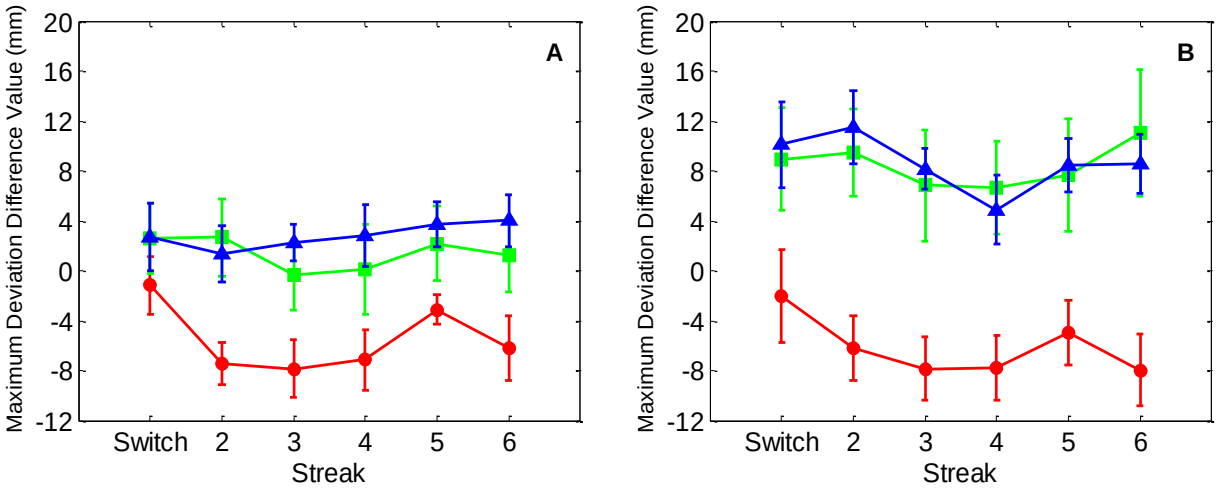

Fig. 3.9. Standardised maximum deviation difference scores (red = AtDCS, green = StDCS, blue = CtDCS) for during-tDCS (A) and post-tDCS (B). Error bars reflect between-subjects S.E.M.

Importantly, standardised scores for MD showed a main effect of stimulation for both during- (Fig. 3.9A; $F(2,24)=4.71$, $p=0.02$, $\eta^2=0.28$) and post-tDCS (Fig. 3.9B; $F(2,24)=8.38$, $p=0.002$ $\eta^2=0.41$) sessions. Fig. 3.9A shows there was a significant reduction in deviation at during-AtDCS compared to during-StDCS ($t(16)=2.22$, $p=0.04$) and during-CtDCS groups ($t(16)=4.57$, $p<0.001$). This reduction in deviation in the AtDCS group was maintained 30 minutes later at post-tDCS (Fig. 3.9B; $t(16)=3.13$, $p=0.006$ and $t(16)=4.32$, $p=0.001$, versus StDCS and CtDCS, respectively). However, as shown by the raw MD data in Fig. 3.8, this maintenance effect is enhanced by decay in performance post-StDCS and post-CtDCS in combination with the maintenance of improvement post-AtDCS. No differences were observed between StDCS and CtDCS standardised scores at either during- ($t(16)=1.08$, $p>0.250$) or post-tDCS ($t(16)=0.01$, $p>0.250$). Thus, in terms of MD we see anodal stimulation of the motor cortex improving performance compared to cathodal and sham stimulation. It should be noted that weaker cathodal compared to anodal effects have been reported previously in tDCS-behavioural studies (e.g. Nitsche, Schauenburg, Lang, Liebetanz, Exner et al., 2003; Spiegel, Hansen, Byblow, & Thompson, 2012).

If, as proposed, anodal tDCS is strengthening the predictable PoP effect then the data should show an increase in MD on the switch trials at during- and post- compared to pre-AtDCS. In other words, there should be a rebound effect on the trials where an unexpected change in target colour occurs. There is a hint of this rebound effect in the standardised MD values presented in Fig. 3.9 where the effect of anodal tDCS approaches zero on the switch trial. To further investigate this rebound effect we split the participants into two groups, high precision and low precision, based on their mean MD at streak 6 compared to the median MD value at streak 6 across all participants (i.e. a median split). The rationale for this was that those participants that naturally show greater trajectory curvature may have a self-imposed

ceiling as to how much deviation their reach could exhibit. Thus, even when the colour does switch MD cannot rebound to a higher level. In contrast, the lower deviation intrinsic to the high precision group should leave scope for the expected crossover effect to occur. A lack of statistical power (n=4) meant that a session x streak interaction for the high precision group failed to reach significance (p=0.11). Nevertheless, as shown in Fig. 3.10A, the high precision participants exhibit the expected rebound effect: there is a reduction in deviation during-AtDCS (and to some extent post-tDCS) on target colour repeat trials, yet this performance enhancement results in a detrimental effect on the switch trial where during- and post-tDCS show considerably greater deviation than pre-tDCS. Thus, when initial performance is good, it allows for PoP to have both positive and negative repercussions.

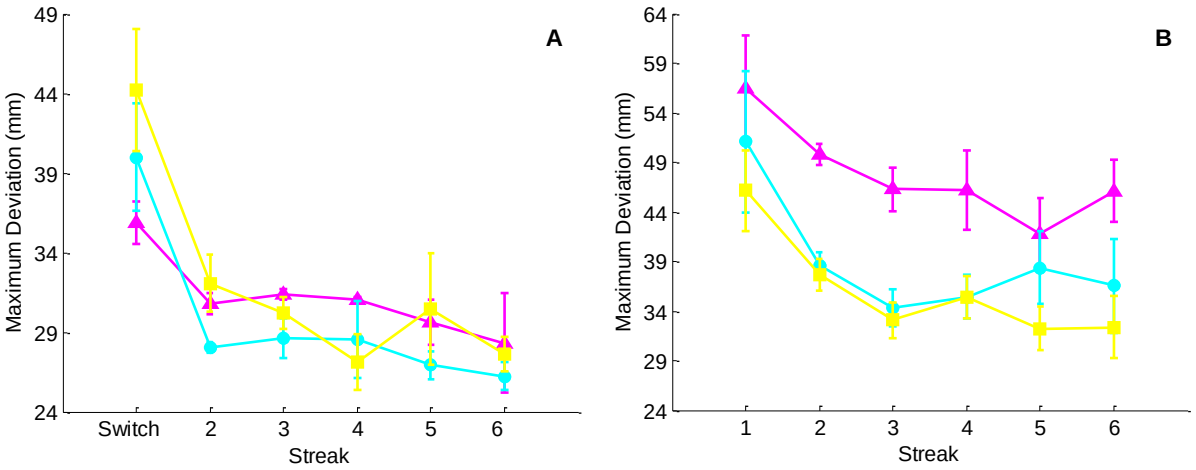

Fig. 3.10. Raw mean maximum deviation values for AtDCS participants split into high precision (A) and low precision (B) groups. Pre-AtDCS performance is shown in magenta, during-AtDCS in cyan and post-AtDCS in yellow. Error bars reflect within-subjects standard error (Cousineau, 2005).

IL did not differ between high and low precision groups ($F(1,7)<1$, $p>0.250$, $\eta_p^2=0.01$) when entered into a 3-way ANOVA with factors precision, session, and streak. This

suggests that the differences between high and low precision groups are not the result of a speed accuracy trade-off. The expected priming effect was present on IL ($F(5,35)=4.04$, $p=0.005$, $\eta_p^2=0.37$) but no other main effects or interactions were observed (ps>0.1).

Finally, supplementary analysis was conducted on the time at which maximum deviation occurred (as a percentage of the movement period). This was to rule out an alternative theoretical explanation for the results based on pre-planned trajectories (see 3.4 for details). There was no main effect of session ($F(2,48)=0.13$, $p>0.250$, $\eta_p^2=0.005$) or stimulation ($F(2,24)=0.12$, $p>0.250$, $\eta_p^2=0.01$), but a main effect of streak ($F(5,120)=3.00$, $p=0.014$, $\eta_p^2=0.11$) with MD getting slightly later as target colour repeated (e.g. streak 2=42.4%, streak 6=41.5%; $t(26)=3.17$, $p=0.004$).

3.2.4 Discussion

Results showed that AtDCS reduced MD over the course of target colour repetitions, strengthening the PoP effect. In other words, where predictability is high, modulation of motor cortex activity improves our ability to select and localise a movement target. However, the IL of the reach was immune to tDCS effects. This is discussed further in section 3.4.

Experiment 3.3: The Effects of tDCS in a Predictable Target Key-press Task

3.3.1 Introduction

The PoP-CRT design of Experiment 2.2 and 3.2 was originally based on the key-press task of Maljkovic and Nakayama (1994). Experiment 3.3 aims to replicate their findings and, in doing so, test whether a motor cortex tDCS effect can be found without requiring an overt reaching movement to achieve the target. Current evidence makes conflicting predictions. On

the one hand a large number of neuroimaging studies (see Kristjansson & Campana, 2010; for a review) failed to report motor cortex activity during primed search tasks. On the other hand, the sequence prediction task used by Schubotz and von Cramon (2002) showed recruitment of the motor system, as did Bestmann et al. (2008) despite the target signalling an arbitrary key-press.

3.3.2 Method

Participants. 18 University of Birmingham students were randomly assigned to either an AtDCS (n=9, 3 males, aged 18-23 (21.9)) or StDCS (n=9, 4 males, aged 18-20 (18.6)) stimulation group.

Behavioural task & data analysis. The task was derived from that of Maljkovic and Nakayama (1994). Participants were presented with displays consisting of 3 diamonds with a 'cut-off' section on either the left or right. The task was to discriminate the side of the cut-off section on the odd-colour item, pressing 'H' on a keyboard if the right side was cut-off and 'B' if the left side was cut-off. Participants completed 8 blocks of 96 trials in each session (pre-, during-, post-tDCS). Both this task and the CRT have been shown to rely on focal attention (Song and Nakayama, 2006). The same streaks of target colour repetitions were embedded as in Experiment 3.2. Dependent variables were raw and standardised reaction times (during- and post- minus pre-tDCS; RT) and accuracy of discrimination of the cut-off side.

3.3.3 Results

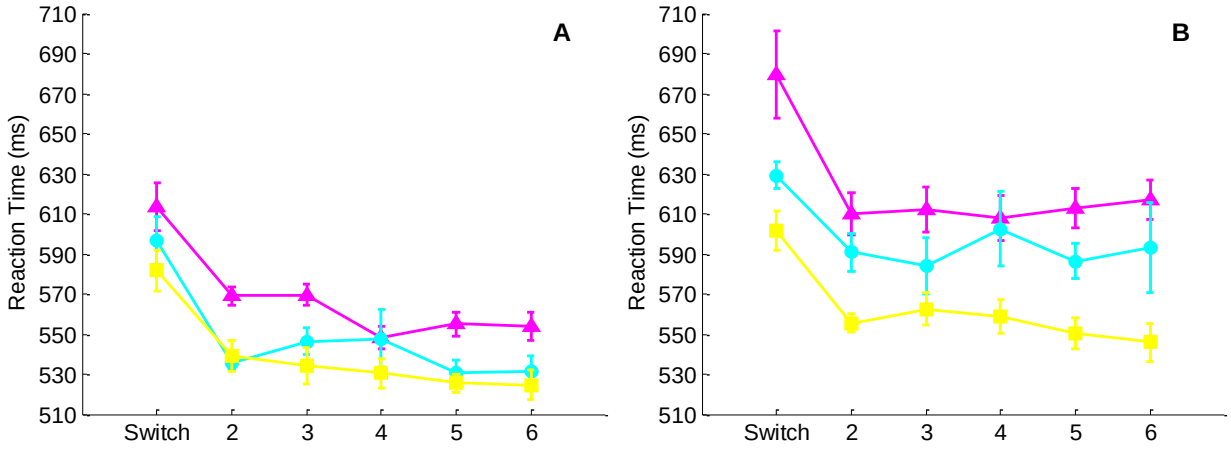

Fig. 3.11. Raw mean RTs for AtDCS (A), and StDCS (B). Pre-tDCS performance is shown in magenta, during-tDCS in cyan and post-tDCS in yellow. Error bars reflect within-subjects standard error (Cousineau, 2005).

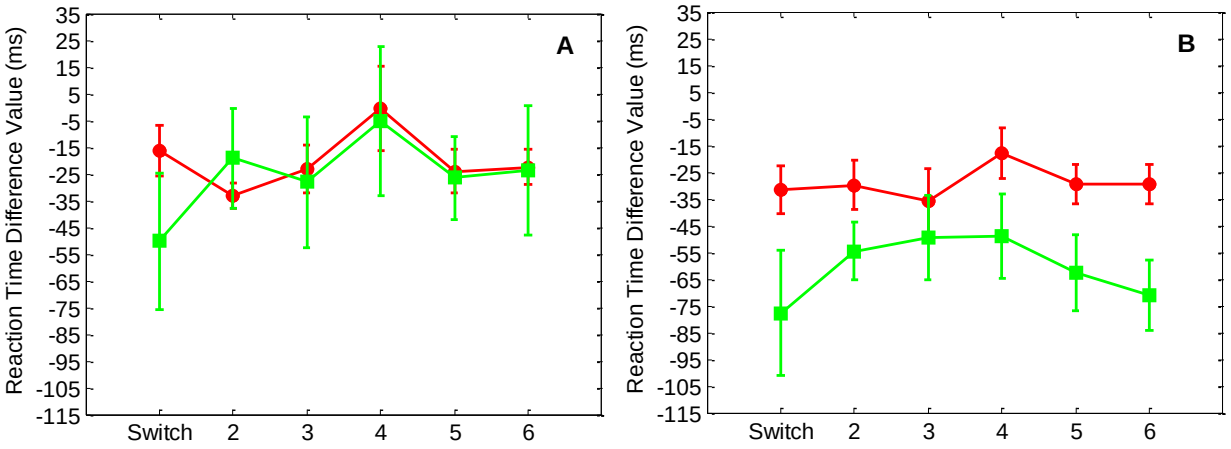

Fig. 3.12. Standardised RT difference scores (red = AtDCS, green = StDCS) for during-tDCS (A) and post-tDCS (B). Error bars reflect between-subjects S.E.M.

Results were collapsed across target colour, position and cut-off side. There were no differences in accuracy according to stimulation ($F(1,16)=0.51$, $p>0.250$, $\eta_p^2=0.03$), session ($F(2,32)=0.07$, $p>0.250$, $\eta_p^2=0.004$), or streak ($F(5,80)=1.45$, $p=0.22$, $\eta_p^2=0.08$), and no interactions. Error trials (3.2%) were then removed prior to RT analysis.

Main effects of session ($F(2,32)=12.16$, $p<0.001$, $\eta_p^2=0.43$; pre-tDCS slowest, post-tDCS fastest and during-tDCS intermediate, ps<0.05) and streak ($F(5,80)=24.61$, $p<0.001$, $\eta_p^2=0.61$; switch trial = 617ms, streak 6 = 561ms; $t(17)=5.20$, $p<0.001$)) were observed on raw RTs indicating practice and priming effects, respectively (Fig. 3.11). There were no significant simple effects of stimulation on standardised RTs either during- (Fig. 3.12A; $F(1,16)=0.06$, $p>0.250$, $\eta^2=0.004$) or post-tDCS (Fig. 3.12B; $F(1,16)=3.99$, $p=0.063$, $\eta^2=0.20$).

3.3.4 Discussion

Stimulation of the motor cortex did not affect PoP when the participants had to make a key-press response, in contrast to the CRT findings of Experiment 3.2. Thus, the motor system was only recruited when the predictable information signalled the target of an overt movement. This explains why previous imaging experiments have failed to show motor cortex activity during key-press PoP tasks (Kristjansson & Campana, 2010), but conflicts with the findings of Bestmann et al. (2008) and Schubotz and von Cramon (2002).

3.4 General discussion

In this chapter we tested whether the motor system contributes to prediction-based guidance of target selection. The results suggest motor system involvement in the selection of predictable colour-defined movement targets. Anodal tDCS was shown to strengthen the PoP

effect when target colour repeats were predictable (Experiment 3.2). Conversely, modulation of motor system activity did not influence behaviour when the target was unpredictable (i.e. chance-level repeats; Experiment 3.1), or when a key-press rather than a reaching response was required (Experiment 3.3). This is in accordance with recent research highlighting the role of the motor system in tasks requiring perceptual prediction (e.g., Bestmann et al., 2008; Schubotz & von Cramon, 2002), and more generally with evidence of motor system involvement in perceptual/attentional processing (e.g., Ostry et al., 2010; Baldauf & Deubel, 2010). The present findings are particularly intriguing considering the systematic predictability pertains to the target colour rather than its location.

There are three possible mechanisms for the motor system predictability effect. Firstly, stimulation of the motor cortex might strengthen the encoding of the predictable information in a bottom-up fashion. With each target repeat the pre-onset activation achieved by the target increases to the point where it effortlessly 'pops-out' and a straighter reach trajectory can be executed. Consistent with this viewpoint, de Lange et al. (2013) showed that the predictability of an upcoming stimulus biases motor cortex activity *before* stimulus presentation. This means that prior probability modifies the starting point for the activation accumulation rather than the threshold at which the decision is made or the speed at which evidence accumulates. However, altering the starting level of activation would presumably affect the initiation of the movement rather than its trajectory. This was shown not to be the case in Experiment 3.2 (see below for further discussion), and argues against this hypothesis.

The second possibility is that the motor system is sensitive to the top-down probability of a target repeat. This would also explain the findings of Bestmann et al. (2008) that demonstrated how pre-stimulus motor cortex activity is biased by the average uncertainty pertaining to a cued target over the course of a trial block. On blocks of trials where the cue

reliably predicts the target (i.e. on 85% of trials) motor cortex activity is higher than on blocks where the cue is less valid (i.e. on 55% of trials). Furthermore, the top-down explanation would be consistent with Baldauf and Deubel's (2010) theory of "visual preparation". Their theory suggests that the feedback connections from motor regions guide attention to extract movement-relevant information from visual stimuli. This guidance occurs in a top-down manner according to the weight attached to the visual inputs from potential movement targets. To speculate, in the present experiments it is possible that the top-down weight attached to the visual input is biased according to the target colour built-up over the previous trials.

Finally, and related to the previous point, tDCS may have modulated the strength of feedback signals from the motor system to posterior parietal regions previously implicated in PoP (e.g. Muggleton, Kalla, Juan, & Walsh, 2011; Taylor, Muggleton, Kalla, Walsh, & Eimer, 2011). This is consistent with a recent investigation by Notturno et al. (2014) that showed M1 tDCS modulated low alpha desynchronisation in parietal regions. Such desynchronisation is typically associated with attentional processing (see Klimesch, 2012; for a review).

One of the questions that remains to be answered is why tDCS modulated MD but not IL in Experiment 3.2. This dissociation could be explained by a methodological factor. To ensure that the reach trajectories reflected ongoing rather than completed target processing participants were instructed to commence their reach before a warning tone 400ms post-stimulus onset. It is possible that this warning tone homogenised ILs across stimulation groups, as supported by ILs that are just below 400ms in each group. However, also note that the 400ms tone was present in previous experiments reported in this thesis without this homogenisation occurring. Another explanation is that reach trajectories are simply more sensitive to the effects of tDCS than reach latencies. This study is not the first to show a lack

of motor system tDCS effects on movement latencies but an effect on later movement parameters such as end-point error and trajectory control (e.g. Galea, Vazquez, Pasricha, Orban de Xivry, & Celnik, 2011; Hunter, Sacco, Nitsche, & Turner, 2009). We have attempted to interpret this dissociation using a computational model (CoRLEGO; Strauss, Woodgate, Sami, & Heinke, in submission). CoRLEGO separates the determination of the odd-colour item and the localisation of the target into two distinct processes. It postulates that the start of the movement is determined by the detection of the odd colour; irrespective of whether the localisation of the target is complete (i.e. the movement is initiated when the target colour is known but not its location). Because localisation is incomplete curved reach trajectories are produced. To simulate the tDCS results CoRLEGO assumes that colour information from the previous trial is stored in both M1 and PPC (consistent with Baldauf & Deubel, 2010). However, it is the stored information in PPC that determines when the movement begins. Thus, IL is not affected by motor cortex tDCS. Following initiation, the localisation of the target relies on the motor system and incoming information from the PPC (see Resulaj et al., 2009; for evidence for a continuous processing pipeline influencing motor behaviour). Thus, only the trajectory of the movement (i.e. post-initiation) is affected by tDCS over the motor cortex.

It is important to note that our interpretation of the present results is strongly based on the assumption that reaching trajectories are not fully pre-planned. Instead, the execution of the movement is continuously influenced by the selection process (c.f. Song and Nakayama's (2009) "leakage" hypothesis). However, there is an alternative theoretical framework (e.g. Stewart, Baugh, Gallivan, & Flanagan, 2013) that suggests that the brain first plans the trajectory to all possible targets and begins executing an "averaged" trajectory before the final target is known to the motor system. In their paradigm participants are signalled the target

after they start moving. In our design the theory of several pre-planned trajectories may play out as follows. After a few trials participants know the potential positions of target and distractors and thus can pre-plan the three possible trajectories. It is therefore possible to initiate the movement towards the centre of the display before selective attention identifies the target and the corresponding planned trajectory is executed. This offers another explanation for the lack of tDCS effect on IL: The reach is initiated to the centre of the display without considering the target identity or location. However, if participants were using this strategy we would expect to see an effect of tDCS on the time at which MD occurs and not just the magnitude of MD. MD should become earlier as a result of AtDCS since focal attention is drawn away from the average of the three positions and towards the target more quickly. Supplementary analysis rendered this unlikely since there was no effect of stimulation on the time at which maximum deviation occurred (see 3.2.3). This argues against the pre-planned trajectory hypothesis in favour of the continuous competition hypothesis.

Another intriguing finding from this chapter is the lack of tDCS effect on RTs in Experiment 3.3. As stated previously, the motor system may only be recruited when the predictable target signals the end-point of an overt movement (for supporting evidence see Adam, Parthoens, & Pratt, 2006; Eisenberg et al., 2011; Festman, Adam, Pratt, & Fischer, 2013). Furthermore, there are many neuroimaging studies that fail to show motor system activation in key-press PoP tasks (see Kristjansson & Campana, 2010). However, the contradiction between the null key-press results presented here and the results of Bestmann et al. (2008) and Schubotz and von Cramon (2002) still remains. Further research would be required to explain the discrepant results, particularly focusing on methodological differences. For instance, in both Bestmann et al. (2008) and Schubotz and von Cramon (2002) the participant was explicitly instructed to learn the predictive nature of visual stimuli whereas

PoP relies on implicit prediction. The role of the motor cortex in implicit learning is well documented (see Nitsche et al. (2003) for M1 tDCS enhancement of implicit sequence learning). However, such implicit learning typically relates to overt movement sequences where visual information is directly related to the motor response (as in the serial reaction time task; Robertson, 2007). It is possible that arbitrary key-press tasks show motor system modulation only when the task involves explicit prediction. If the learning is implicit then an overt movement may be required to see any effect of tDCS. Also, Schubotz and von Cramon (2002) modulated activity in premotor cortex, which is important for task-related planning independent of the method of response (e.g. Baker, Rogers, Owen, Frith, Dolan, et al., 1996), rather than the primary motor cortex that was targeted in the present experiments. In fact, the lack of RT effect in Experiment 3.3 helps to overcome a criticism of tDCS based on its low spatial precision, i.e. if premotor activity was being unintentionally modulated then we would expect an effect on key-press responses.

In summary, choice reaching trajectories were straighter when tDCS was applied over the motor cortex, but only if the target colour was predictable. This supports a role for the motor cortex in prediction-based guidance of target selection. Furthermore, the results from Experiment 3.3 suggest that the perceptual information must be movement-relevant, in this case signalling the end-point of a reach. These conclusions are consistent with recent literature that highlights the role of the motor system in processing previously thought to be completed at an earlier neural stage.

CHAPTER 4

Global-to-local Scene Processing Affects Visually-guided Manual Reaching

4.0.1 Abstract

It is widely believed that visual scenes are processed in a global-to-local fashion. This paper examined whether visually-guided reaching movements also reflect this processing strategy. A choice reaching task (CRT) was employed where participants reached to an odd-colour target. Global information was manipulated by changing the arrangement of the search items (configuration). Local information was manipulated by the target/distractor positions. We analyzed how reaches to targets were affected by priming from preceding trials. Two experiments revealed that the initiation of the movement was modulated by configural priming (global-level), whereas the later movement phase (trajectory deviation) was influenced by position priming (local-level). Thus, global-to-local processing may be reflected in reaching movements. Furthermore, priming probability influenced position priming but not configural priming. This suggests global processing relies on bottom-up computation whilst local processing is top-down modulable. The findings highlight the utility of the CRT for investigating the characteristics of global-to-local processing.

4.0.2 Introduction

It is generally believed that we perceive the global aspect of a scene prior to its local features. For instance, when we enter a building we quickly realize that we are in a pub but only later become aware of the locations of the bar, the glasses, the toilets, etc. This assumption is supported by numerous findings from behavioural studies in visual search (Conci, Müller, & Elliott, 2007), hierarchical figures (Navon, 1977), scene categorization (Schyns & Oliva, 1994), and face processing (Maurer, Le Grand, & Mondloch, 2002) and from neuroimaging studies using fMRI (e.g. Goffaux, Peters, Haubrechts, Schiltz, Jansma, & Goebel, 2011) and ERPs (Conci, Töllner, Leszczynski, & Müller, 2011). This processing strategy is often

characterized as "global-to-local" or "coarse-to-fine" (see Hegde, 2008; and Hochstein and Ahissar, 2002; for theoretical frameworks). Until now, evidence for this strategy stemmed from key-press response tasks. In this chapter we explore whether this processing cascade is also reflected in simple reaching movements. For instance when reaching for a target item the initiation of the movement may be influenced by global information whilst the later movement phase (e.g. characteristics of reach trajectories) may be governed by local information (i.e. the target location). Such influences are a distinct possibility based on recent studies showing that cognitive processes (e.g. language processing; Spivey, Grosjean, & Knoblich 2005; numerical representation; Song & Nakayama, 2008) can "leak" into reaching movements (see Song & Nakayama, 2009; for a review; and Strauss & Heinke, 2012; for a computational model). Therefore the present chapter explores whether the global-to-local cascade in processing of visual information can leak into visually-guided reaching movements.

A study by Song and Nakayama (2006) has already demonstrated that reaching trajectories can be affected by somewhat local visual information. In their choice reaching task (CRT) participants were asked to reach and touch an odd-colour target (green item among two red items, or vice versa) on a computer monitor. The target location varied randomly but there were systematic repetitions of target colour ("streaks") embedded within the trial blocks. They found that the colour streaks reduced the curvature of the reach trajectory. However, when the colour switched after a streak curvature increased – the reach was initially directed towards a distractor before being corrected mid-flight. Hence, trajectory curvature (i.e. the maximum deviation of the trajectory from a straight line path; MD) reflected local information processing. Note that Song and Nakayama (2008) showed that these curved trajectories are the result of corrections occurring very soon (around 125 ms)

after movement initiation. This is consistent with recent findings from a broad range of reaching experiments showing modifications of trajectories during a movement phase that was previously thought to be immune to such changes (i.e. initial ballistic movements; see Elliott, Hansen, Grierson, Lyons, Bennett, & Hayes, 2010; for a review). The same colour priming effect was also observed on the initiation latency (IL) of the movement. It is important to note that these IL/MD patterns replicate colour priming effects found in earlier reaction time (RT) studies (e.g. Maljkovic & Nakayama, 1994), i.e. RTs decreased with the repetition of the target colour but increased when the colour switched.

If the reaching process is also affected by global-to-local processing of visual information it is conceivable that priming on the two levels is differentially reflected in IL and MD. To be more specific, the later MD should exhibit local priming effects, as shown by Song & Nakayama (2006), while the early IL should reflect a priming effect on the global level. Thus, we should be able to demonstrate a dissociation between IL and MD. Song and Nakayama's (2006) study was not able to demonstrate such a dissociation as they did not systematically manipulate global display properties. A basic global characteristic is the configuration of the items. Song & Nakayama's design used a triangular configuration. Our new design introduced an additional configuration – an inverted triangle (see Fig. 4.2). As a result, we expected repetition of the configuration to speed ILs whilst switching the configuration should result in delayed reach onset (configural priming). For the local-level, we realized that colour priming could be seen as tapping into somewhat global processing as it could activate groups of distractors rather than individual (i.e. local) items. Therefore we removed the colour streaks and instead explored whether changes in local target position (position priming; Geyer and Müller, 2009) affected MD. This way the experiment operationalizes the two levels with more distinguishable manipulations. There were three

position priming conditions. First the target position could repeat from one trial to the next (target condition). Second the target could appear at a location previously held by a distractor (distractor condition). Finally, the target could appear at a previously unoccupied location (empty condition). Geyer and Müller's (2009) key-press experiments found RTs were fastest in the target condition, intermediate in the empty condition and slowest in the distractor condition (see also Maljkovic & Nakayama, 1996). Given the link between MD and RTs established in Song & Nakayama's (2006) study we expected MD to be modulated by position priming in the same way: The previous target position should show least curvature, the previous distractor position the most curvature, with the previous empty location acting as a neutral baseline. So how does this prediction for MD relate to the predictions for IL? As we expected IL to reflect configural priming, IL should be unaffected by previous target/distractor positions as they occur within the same configuration. In contrast, IL should be disrupted when the configuration changes. In the present design this configuration switch corresponds to an empty condition. Thus we expected the empty condition to result in a slower response compared to both target and distractor conditions, representing the dissociation between IL and MD referred to earlier.

To foreshadow our results, using a key-press paradigm Experiment 4.1 confirmed that configural priming modulated global-level processing whilst position priming modulated local-level processing. Experiment 4.2 demonstrated that configural and positional biases modulated IL and MD, respectively. Thus the CRT is able to reflect the global-to-local cascade in processing of visual information. We aimed to replicate and extend our findings in Experiment 4.3. In Experiment 4.2 the ratio of position priming trials was balanced while configural priming was unbalanced. Experiment 4.3 investigated whether the same configural and positional effects were exhibited when this imbalance was reversed (i.e. when an equal

configural priming ratio caused an unequal position priming ratio). Whilst configural priming was unaffected, position priming effects were modulated by switch-repeat probabilities. Finally, Experiment 4.4 added another search item creating square/diamond configurations. Configural priming was still present but the effects of distractor inhibition began to modulate ILs. This suggests that the speed at which global- and local-level representations are formed is determined, at least in part, by the properties of the global structure.

Experiment 4.1: Key-press Control Studies

4.1.1 Introduction

Before examining whether the CRT is able to tap into early and late scene processing we must confirm that configural and position priming influence global and local processing, respectively. To do so, we conducted two baseline experiments where we deliberately employed task-setting restrictions to force participants to attend globally or locally. In Experiment 4.1.1 we used a target detection paradigm whereby the participant simply reports the presence/absence of the odd-coloured item. Such detection tasks have been shown to rely on distributed attention (Bravo & Nakayama, 1992). If configural priming is an early, global-level process then detection RTs should be expedited when the configuration repeats and slowed when the configuration switches. This would also represent the first demonstration that present/absent decisions are sensitive to the configuration of the search items.

In Experiment 4.1.2 participants were presented with a compound discrimination task where a response must be made based on a target feature (i.e. the location of a cut-off segment). Such discrimination has been shown to rely on local-level focal attention (Maljkovic & Nakayama, 1994). Based on previous research (e.g. Geyer & Müller, 2009),

RTs should be fastest when the target position repeats and slowest when the target appears at a previous distractor position compared to a previous empty position.

Experiment 4.1.1: Configural Priming Modulates Global Detection

4.1.1.1 Method

Participants. 15 participants were recruited from the undergraduate population at the University of Birmingham (6 male, aged 18-31 (mean 19.9)). All participants were right-handed with normal colour vision and normal or corrected-to-normal visual acuity. Written informed consent was obtained from participants prior to starting the experiment.

Procedure, design & analysis. Participants completed 8 blocks of 96 trials. On each trial three truncated diamonds were presented (see Experiment 3.3; Maljkovic and Nakayama, 1994) in a triangular or inverted triangular configuration. Participants had to respond to the presence/absence of an odd-coloured item amongst two homogenously coloured distractors, pressing 'H' if the target was present and 'B' if the target was absent. They were instructed to complete the task as quickly and as accurately as possible.

The triangular configuration of the stimuli was equally likely to switch or repeat. The number of present/absent trials and the target colour (in present trials) was pseudorandomly selected to ensure a 50-50 split of each. Target absent trials acted as fillers and were discarded prior to analysis. The dependent variables detection accuracy and RT were subject to paired-samples t-tests comparing configuration switches vs. repeats.

4.1.1.2 Results

Results were collapsed across target colour and position and outliers – trials with RTs greater than 2 standard deviations from the mean per participant (2.5% of trials) – were removed.

There was no difference in accuracy between configuration switches and repeats. Incorrect responses were removed from further analysis (3.0% of trials). RTs were faster on trials where the configuration repeated versus when the configuration switched (432ms vs. 426ms; $t(13)=2.20$, $p=0.046$, $d=0.59$). Thus, configural priming influenced rapid detection relying on distributed, global-level processing.

Experiment 4.1.2: Position Priming Modulates Local Discrimination

4.1.2.1 Method

The method remained the same as that presented in Experiment 4.1.1 with the following exceptions.

Participants. 11 new participants were recruited from the undergraduate population at the University of Birmingham (2 male, aged 18-21 (18.9)).

Procedure, design & analysis. Participants were required to discriminate a secondary feature of the odd-colour target (i.e. a compound search task; Maljkovic & Nakayama, 1996). Again, the participant had to search for the odd-colour diamond, this time pressing 'B' if the left side was cut off and 'H' if the right side was cut off (2° cut-off segment on 3.5° x 3.5° diamond). Participants were instructed to complete the task as quickly and as accurately as possible.

Dependent variables were accuracy (cut-off discrimination) and RT (correct trials only). These dependent variables were subject to a one-way ANOVA with the sole factor position priming (previous target vs. previous empty vs. previous distractor positions) and a

paired-samples t-test analysing effects of configural priming (switch vs. repeat). The ratio of configuration repeats versus switches was 1:1.

4.1.2.2 Results

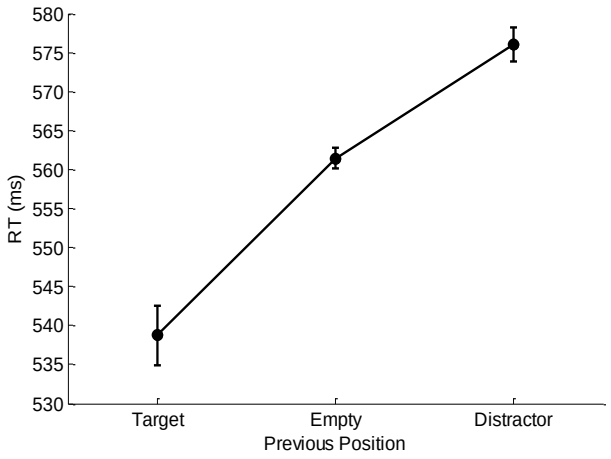

Fig. 4.1. The effect of position priming on RTs in a compound search task. Error bars represent within-subjects S.E.M (Cousineau, 2005).

Results were collapsed across target colour and position and outliers (1.9% of trials) were removed.

There was no difference in accuracy between configuration switches and repeats, or between position priming levels. Incorrect responses were removed from all further analyses (3.9% of trials). RTs were unaffected by configural priming (switch = 561ms, repeat = 563ms). In accordance with our hypothesis that stimulus configuration modulates early processing, we tested whether those with faster key-press RTs showed any evidence of configural priming using a within-subjects median split. A two-way ANOVA with factors RTsplit (fast vs. slow) and configural priming showed no main effect of configural priming but there was a configural priming x RTsplit interaction ($F(1,10)=7.81$, $p=0.02$, $\eta_p^2=0.44$).

However, this resulted from the slow group having longer RTs in repeat trials versus switch trials (644ms vs. 640ms; $t(10)=2.88$, $p=0.016$).

RTs were affected by position priming ($F(2,20)=37.66$, $p<0.001$, $\eta^2=0.79$), replicating Geyer and Müller (2009; Fig. 4.1). Target repeats had shorter RTs than previous empty ($t(10)=5.34$, $p<0.001$) and distractor trials ($t(10)=6.54$, $p<0.001$), with previous empty trials also having shorter RTs than previous distractor trials ($t(10)=6.13$, $p<0.001$).

4.1.2 Discussion

Experiment 4.1.1 demonstrated that configural priming modulates global-level processing (i.e. the detection of a stimulus). Thus, if our prediction that reaching movements reflect the global-to-local cascade of processing is correct, then the IL of the reach movement should be modulated by configural priming.

Experiment 4.1.2 replicated the results from previous studies showing position priming effects in a local discrimination task (e.g. Geyer & Müller, 2009; Maljkovic & Nakayama, 1996). Again, if reaching movements are influenced by global-to-local scene processing, any local-level position priming effects should affect later indices of behaviour, namely MD.

Experiment 4.2: Global-to-local Scene Processing Affects Manual Reaching Movements

4.2.1 Introduction

Experiment 4.2 aimed to test whether configural priming and position priming map onto temporally distinct outcome measures - the initiation latency of the reaching movement (IL) and the maximum deviation of the reach trajectory (MD).

4.2.2 Method

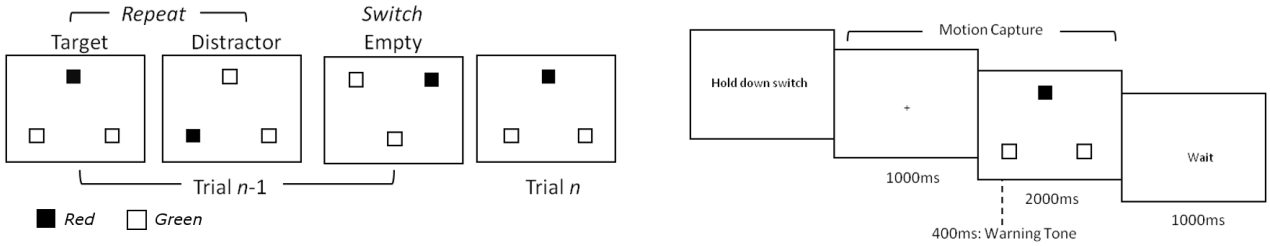

Fig. 4.2. Schematic illustration of the experimental design. Left: Configural and position priming conditions. The position priming conditions 'Target', 'Distractor', and 'Empty' refer to the identity of the item appearing at the current target location on the previous trial. These position priming conditions combined to create a configuration repeat and a configuration switch condition, shown in italics. Right: Trial Timeline. Pressing a trigger switch commenced each trial with stimuli shown for 2000ms following initial fixation. A warning tone after 400ms encouraged rapid initiation. Motion capture recording began at fixation for 3000ms.

The method matched that of Experiment 2.1 with the following exceptions.

Participants. 22 new participants (6 male), aged 18-20 (mean 19.1) were recruited in exchange for course credit. The number of participants was larger than in previous experiments to ensure that we avoided a Type II error with regards to a position priming effect on IL.

Procedure. An overview of the trial procedure is given in Fig. 4.2. Following fixation participants were presented with three squares (3.8° x 3.8°) positioned at either 12 o'clock, 4 o'clock and 8 o'clock (triangle configuration) or 2 o'clock, 6 o'clock and 10 o'clock (inverted

triangle configuration) around an imaginary ellipse (radius 12.2°). Two of the squares (the distractors) were green and the other square (the target) was red, or vice versa.

Design & analysis. Participants completed 4 blocks of 96 trials with a short break separating each block. Target colour was pseudorandomly allocated on each trial to ensure an equal split of red and green targets. Each block of trials was split equally according to position priming (previous target, previous distractor and previous empty location; Fig. 4.2, left). To assess the effects of configural priming a configuration repeat level was created by combining previous target and previous distractor position priming levels (Fig. 4.2, left). The configuration switch level corresponded to the previous empty position priming level. Note also that collapsing the previous target and previous distractor positions into one configuration repeat level produced twice as many configuration repeat trials as configuration switch trials (comprised solely of 33% previous empty position priming trials).

We analysed position and configural priming effects separately. To investigate the effects of position priming data were analysed in a one-way within-subjects ANOVA with position priming (target vs. distractor vs. empty) as the sole factor. Significant main effects were explored with paired-samples t-tests. Configural priming (switch vs. repeat) was subject to a paired-samples t-test. For both analyses dependent variables were IL and MD. We also analysed the unbalanced conditions (configural priming in Experiment 4.2 and position priming in Experiment 4.3) with a permutation test but found no differences to the analysis with ANOVA. Therefore we report only the ANOVA results.

4.2.3 Results

Prior to analysis any error trials and outliers were removed. Errors included incorrect target responses (i.e. where the participant reached to the wrong colour square; <1%), and motion

capture recording errors (1.7%, including one block of 96 trials from one participant whose remaining data was still analysed). 2.8% of trials were removed as outliers (trials with ILs >2 standard deviations from the mean per participant).

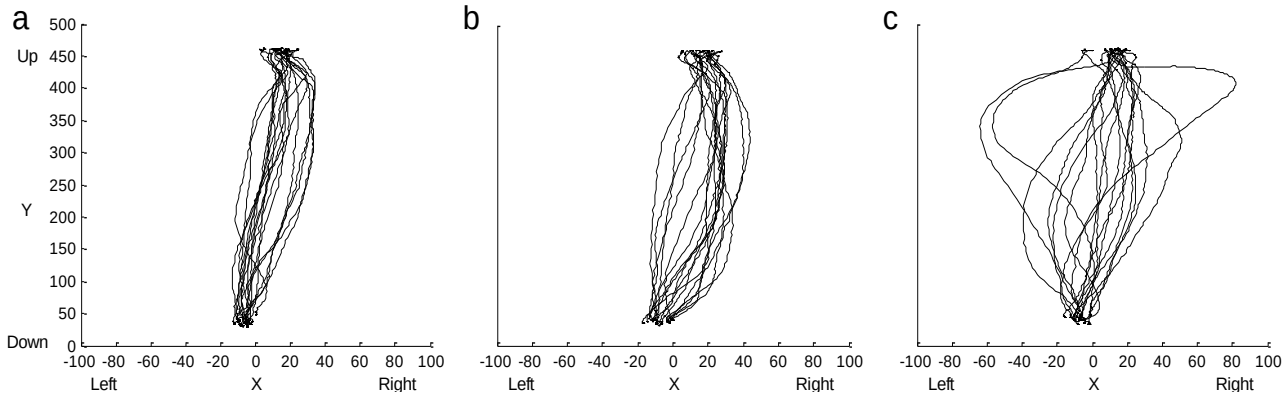

Fig. 4.3. Exemplar reach trajectories (mm; XY) from a representative participant in Experiment 4.2. Each line represents the trajectory of a single trial. Reaches are to the centre/top target for previous target (a), previous empty (b) and previous distractor (c) trials.

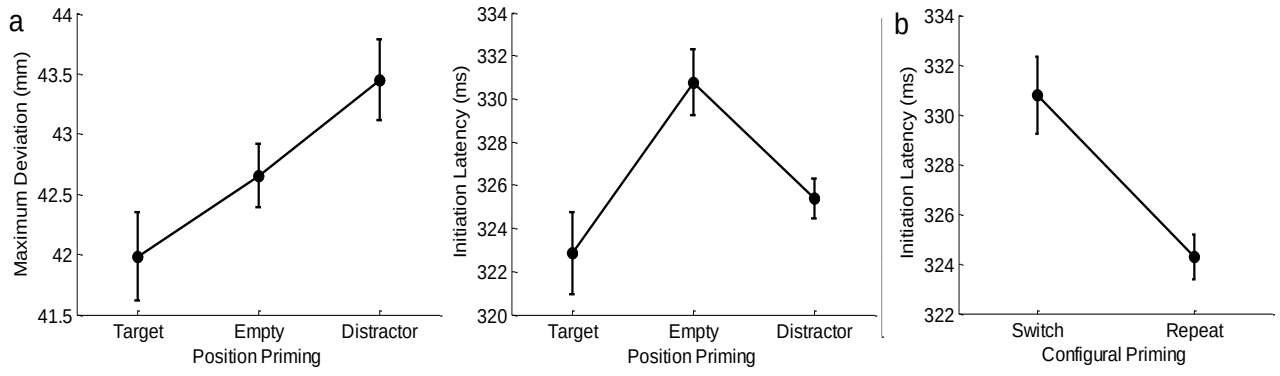

Fig. 4.4. Position priming effects on mean maximum deviation (panel a, left) and initiation latency (panel a, right) and configural priming effect on initiation latency (panel b) in Experiment 4.2. Error bars reflect within-subjects standard error (Cousineau, 2005).

Examples of reach trajectories for previous target, empty, and distractor trials for one participant are shown in Fig. 4.3. Consistent with previous work showing position priming effects on local processing (e.g. Geyer & Müller, 2009) we found a main effect of position priming on MD ($F(2,42)=3.55$, $p=0.038$, $\eta^2=0.14$). The trajectories of reaches to the previous target position were significantly less curved than those to the previous distractor position ($t(21)=2.34$, $p=0.029$; Fig. 4.4a, left), but no different to the previous empty position ($p=0.15$). A significant main effect of position priming was also observed on IL ($F(2,42)=5.37$, $p=0.008$, $\eta^2=0.20$), however the effect was qualitatively different to the MD effect: a target appearing at a previous empty position had longer ILs than both previous target ($t(21)=2.57$, $p=0.018$) and previous distractor positions ($t(21)=2.72$, $p=0.013$; Fig. 4.4a, right). There was no difference between previous target and distractor positions ($p>0.250$). Instead, configuration repeat trials exhibited significantly shorter ILs than configuration switch trials ($t(21)=2.87$, $p=0.009$, $d=0.61$; Fig. 4.4b). There was no significant effect of configural priming on MD (42.85mm vs. 42.66mm; $p>0.250$).

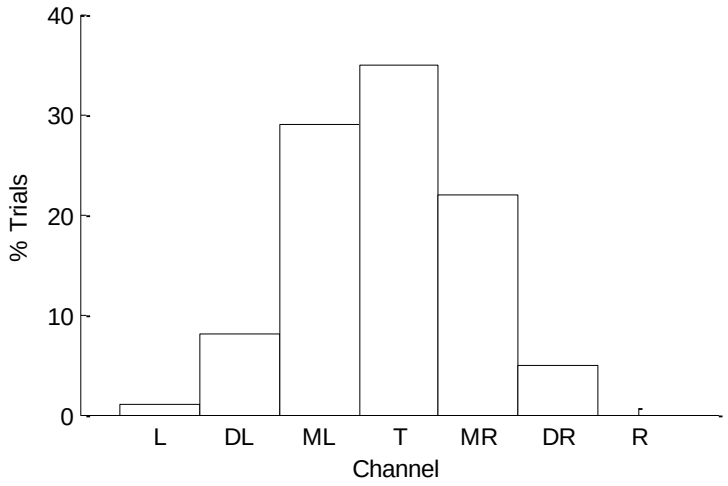

Fig. 4.5. Distribution of initial reach trajectories on configural repeat trials. Analysis follows method described in 2.1.2. with angles calculated at 100mm from starting point. L=Left, DL=Distractor Left, ML=Middle Left, T=Target, MR=Middle Right, DR=Distractor Right, R=Right.

Another plausible explanation might state that the IL results reflect a strategy to randomly select one item in the array and initiate the movement toward that item before the final selection decision is made en route. This would also likely lead to the pattern of configural priming with reaches initiated to one of the three locations presented on the previous trial more quickly than novel locations. However, the distribution of initial reach trajectory angles presented in Fig. 4.5 argues against this strategy. When the configuration repeats it is clear that the reach is initially directed towards the target far more frequently than towards either of the other two search items.

4.2.4 Discussion

Experiment 4.2 showed a different response pattern for IL than for MD. For MD we replicated the position priming effect found by Geyer and Müller's (2009) key-press experiment. In contrast, IL was not affected by previous target position but was most disrupted by a configuration change (i.e. target at a previously empty position). Thus, Experiment 4.2 provides evidence that global-to-local processing affects manual reaching movements.

Experiment 4.3: Sensitivity of Early and Late Processing to Priming Probability

4.3.1 Introduction

Experiment 4.3 set out to replicate the results from Experiment 4.2 with different priming ratios. Presenting equal numbers of position priming trials in Experiment 4.2 meant there were twice as many configuration repeats (i.e. previous target plus previous distractor position

priming trials) versus switches (previous empty position priming trials). Experiment 4.3 balanced the trials according to configural priming probability, which in turn leads to an imbalance in position priming with target repetitions occurring less frequently than previous distractor/empty trials.

4.3.2 Method

The method of Experiment 4.3 matched that of Experiment 4.2 with the following exceptions.

Participants. 13 new participants were recruited from the undergraduate population at the University of Birmingham (3 male, aged 18-22 (mean 19.5)).

Procedure, design & analysis. Within each of the 4 blocks of trials the triangular configuration of stimuli was equally likely to repeat or switch (invert) from one trial to the next. The target was equally likely to appear at any position within the respective configurations. To analyse configural priming effects a paired-samples t-test was conducted comparing switches versus repeats. Subsequently a one-way ANOVA analysed position priming effects by separating configuration repeats into previous target (17% of trials) and previous distractor (33% of trials) trials, and using the 50% configuration switch trials as the previous empty position priming level. Finally, mixed ANOVAs examined differences in IL and MD according to experiment (Experiment 4.2 vs. Experiment 4.3) and configural/position priming.

4.3.3 Results

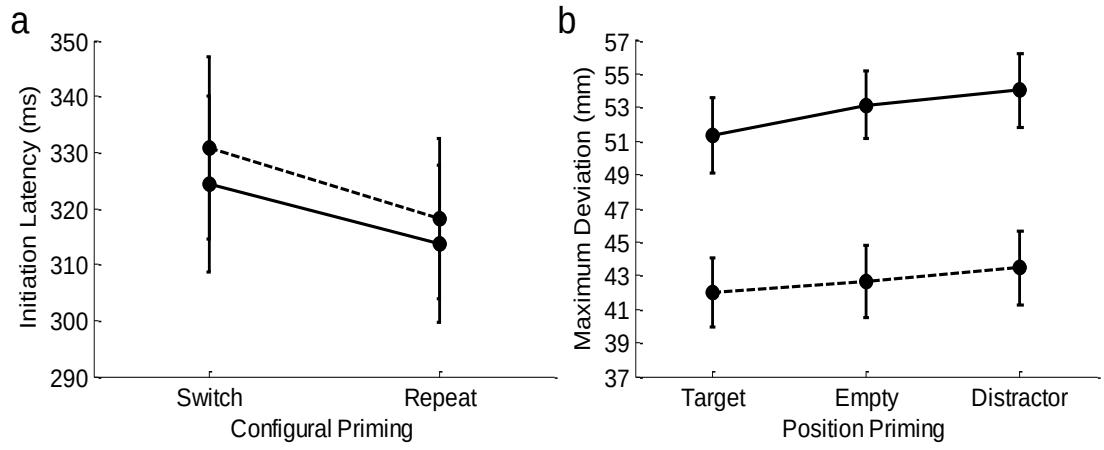

Fig. 4.6. Comparison of initiation latency (a) and maximum deviation (b) effects in Experiment 4.2 (dashed line) and Experiment 4.3 (solid line). Note that here error bars reflect between-subjects S.E.M.

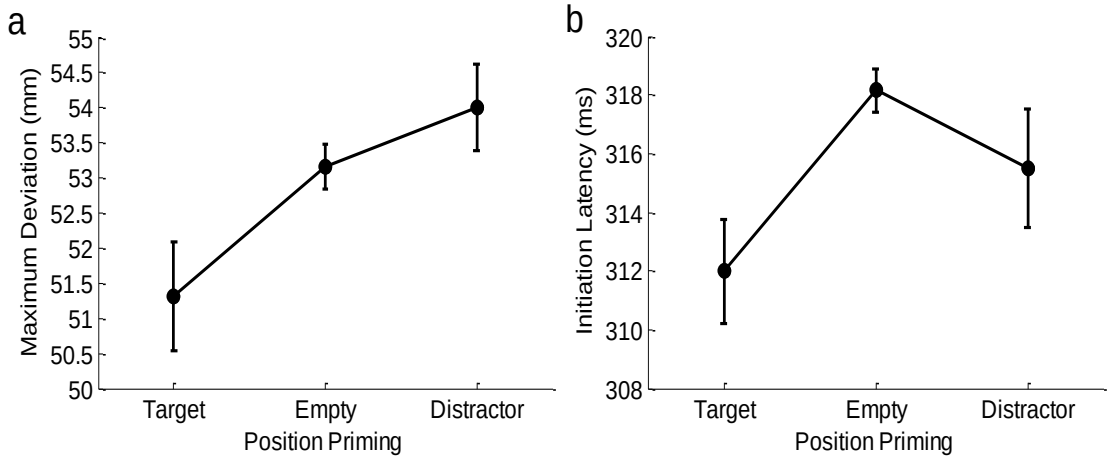

Fig. 4.7. Position priming effects on maximum deviation (a) and initiation latency (b) in Experiment 4.3. Error bars reflect within-subjects standard error (Cousineau, 2005).

Results were collapsed across target colour and position and outliers and error trials were removed (outliers: 2.7%; incorrect target selections: 0.2%; motion capture errors <0.1%).

The pattern of position and configural priming effects were similar to those from Experiment 4.2. ILs were again modulated by configural priming ($t(12)=2.97$, $p=0.012$,

d=0.82) with switches having significantly longer latencies than repeats (Fig. 4.6a, solid line). As in Experiment 4.2, MD was unaffected by configural priming (switch = 53.16mm, repeat = 52.67mm; $p>0.250$). There was a significant effect of position priming on MD ($F(2,24)=3.63$, $p=0.042$, $\eta^2=0.23$; Fig. 4.7a). The previous linear pattern of position priming results was observed with trends for reaches to previous target positions to be less curved than reaches to previous empty positions ($t(12)=1.84$, $p=0.091$), and previous distractor positions ($t(12)=2.14$, $p=0.054$). There was no effect of position priming on IL ($p=0.10$; Fig. 4.7b).

A mixed ANOVA with factors configural priming (switch vs. repeat) and experiment (4.2 vs. 4.3) showed a main effect of configural priming ($F(1,33)=11.85$, $p=0.002$, $\eta^2=0.26$) on IL but no difference between Experiments 4.2 and 4.3 ($p>0.250$) and no interaction ($p>0.250$; Fig. 4.6a). Thus, configural priming had a similar influence on IL regardless of the switch-repeat probability. A second mixed ANOVA with factors position priming and experiment showed a main effect of experiment on MD ($F(1,33)=10.04$, $p=0.003$, $\eta^2=0.23$) with Experiment 4.2 (more target repeats) showing less deviation than Experiment 4.3 (fewer target repeats; 42.70mm vs. 52.83mm, Fig. 4.6b). The main effect of position priming remained significant ($F(2,66)=7.80$, $p=0.001$, $\eta^2=0.19$) with previous target trials (45.45mm) showing less deviation than previous empty (46.56mm; $t(34)=2.36$, $p=0.024$) and previous distractor (47.37mm; $t(34)=3.16$, $p=0.003$) trials, and a trend for previous empty trials to show less trajectory deviation than previous distractor trials ($t(34)=1.58$, $p=0.073$). No interaction between experiment and position priming was observed ($p>0.250$).

4.3.4 Discussion

The global configuration of the stimuli modulated IL and position priming influenced MD, replicating Experiment 4.2's results. Moreover, when comparing Experiment 4.2 with

Experiment 4.3 we found that the probability of encountering a configuration switch/repeat had no influence on ILs whilst an effect of position priming probability was observed on MD – deviation increased when a target repetition was less likely. Hence Experiment 4.3 reinforces the finding from Experiment 4.2 that the CRT can tap into the global-to-local processing strategy. In addition, Experiment 4.3 reveals that the two levels respond differently to a change in priming ratio. This differential finding has an important theoretical implication, as we will discuss in section 4.5.

Experiment 4.4: Generalisation of Configural Priming to 4-item Displays

4.4.1 Introduction

Thus far all experiments have used displays consisting of one target and two distractors. Targets within 3-item displays have been shown to take longer to discriminate (Bravo & Nakayama, 1992) and localise with a reach (Song & Nakayama, 2006) than when surrounded by a greater number of distractors, likely due to increased target-distractor contrast (Sagi & Julesz, 1987) and more effective perceptual grouping (Bravo & Nakayama, 1992) with more search items. Experiment 4.4 tested whether the same global-to-local processing cascade was observed when the number of items increased.

Furthermore, the results of the present experiment will have implications for the CRT methodology itself. In the previous experiments IL was influenced by configural priming, whilst MD was influenced by position priming. The question remains whether IL continues to reflect global level biases when global processing speed increases (i.e. with more search items). It may be that global configural processing is completed too early to coincide with IL.

Instead IL might index later position priming effects in a similar manner to MD results of Experiments 4.2 and 4.3.

4.4.2 Method

The method of Experiment 4.4 matched that of Experiment 4.2 with the following exceptions.

Participants. 13 new participants were recruited from the undergraduate population at the University of Birmingham (2 male, aged 18-21 (mean 19.1)).

Procedure, design & analysis. The configuration of stimuli was equally likely to switch or repeat from trial-to-trial. The target and distractors were positioned in either a square or diamond formation. The diamond was created by positioning the four items at the top, right, bottom and left of an imaginary ellipse of radius 10.4°. The square was created by rotating the diamond shape through 45° to maintain the same inter-stimulus separation. The target was equally likely to appear at any of the four positions within the respective configurations. IL and MD were initially entered into a mixed ANOVA with factors experiment (Experiment 4.3 (3-item) vs. Experiment 4.4 (4-item)) and position/configural priming. Subsequently, position priming within Experiment 4.4 (4-item) was analysed with a one-way ANOVA and a paired-samples t-test compared configuration switches and repeats.

4.4.3 Results

Again, results were collapsed across target colour and position, and error trials were removed (outliers: 1.6%; incorrect target selections: <0.1%; motion capture errors: 0.6%).

Experiment x Position/Configural Priming. The effect of position priming on MD was again significant ($F(2,48)=4.85$, $p=0.012$, $\eta_p^2=0.17$). There was also a main effect of experiment ($F(1,24)=26.68$, $p<0.001$, $\eta_p^2=0.53$) with greater MD in Experiment 4.3 (3-item; 52.83mm)

compared to Experiment 4.4 (4-item; 34.16mm), but no position priming x experiment interaction (p>0.250). Reaches to the previous target position (42.49mm) were less curved than to the previous distractor (44.37mm; t(25)=2.49, p=0.02) and previous empty positions (43.63mm; t(25)=1.86, p=0.075) and reaches to the previous empty position were less curved than to the previous distractor position (t(25)=1.82, p=0.08).

There was a main effect of position priming (F(2,48)=9.98, p<0.001, η_p^2=0.29) on IL but no effect of experiment (p>0.250) or any interaction (p>0.250). When collapsed across experiment ILs were longer on previous empty (310ms) versus previous target (302ms; t(25)=4.33, p<0.001) and distractor trials (306m; t(25)=1.97, p=0.06). However, ILs were also longer on previous distractor trials compared to previous target trials (t(25)=2.52, p=0.019). This is inconsistent with configural priming whereby target and distractor trials should have equally short ILs. This will be explored further in the analysis of Experiment 4.4, below. Nevertheless, there was a main effect of configural priming on IL (switches = 310ms, repeats = 305ms; F(1,24)=12.75, p=0.002, η_p^2=0.35), but no main effect of experiment (p>0.250), and no interaction (p>0.250). MD was unaffected by configural priming, but the main effect of experiment remained significant (F(1,24)=26.56, p<0.001, η_p^2=0.53). The interaction did not reach significance (p>0.250).

Experiment 4.4 – 4-item Configuration. When the target was presented with three distractors there was no effect of position priming on the MD of the reach (p>0.250; Fig. 4.8a left). IL was influenced by position priming (F(2,24)=8.82, p=0.001, η^2=0.42; Fig. 4.8a right). These results again differ from classical position priming results with the previous empty location showing longer ILs than the previous target location (t(12)=3.24, p=0.007) and a trend towards longer ILs than the previous distractor location (t(12)=1.72, p=0.112), broadly consistent with configural priming. However, we also see significantly longer ILs on previous

distractor versus previous target trials ($t(12)=3.46$, $p=0.005$), unlike in the 3-item experiments where repetition of the configuration speeded ILs regardless of the exact previous target position. Thus, the effect of configuration is not as strong as it was with displays featuring one target and two distractors (Experiments 4.2 and 4.3); there is now weaker facilitation when the target appears at a previous distractor position. This explains the significant difference between previous target and distractor positions reported in the mixed ANOVA, above.

Nevertheless, a main effect of configural priming was observed on IL ($t(12)=2.32$, $p=0.039$, $d=0.64$), with configuration repeats having shorter ILs than switches (Fig. 4.8b). MD showed no effect of configural priming (switch = 34.09mm, repeat = 34.46mm; $p>0.250$).

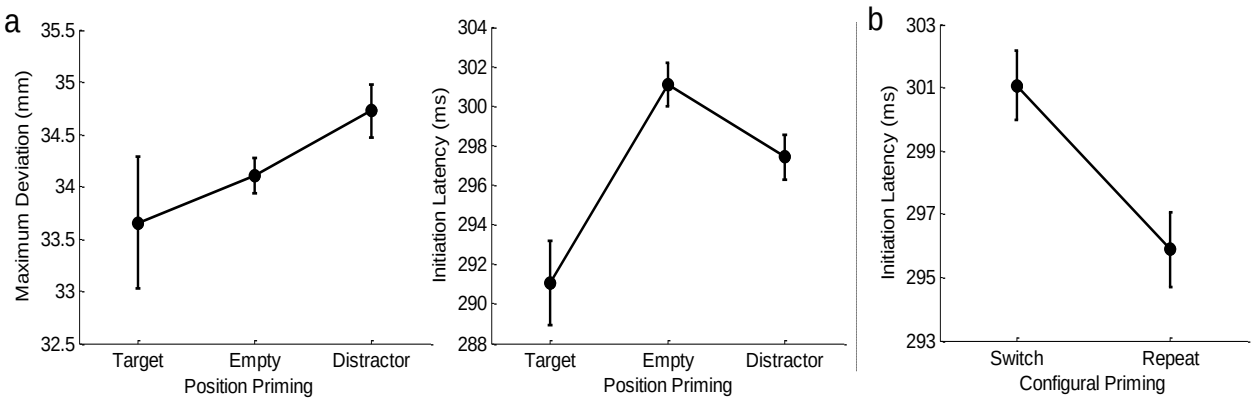

Fig. 4.8. Position priming effects on mean maximum deviation (panel a, left) and initiation latency (panel a, right) and configural priming effect on initiation latency (panel b) in Experiment 4.4. Error bars reflect within-subjects standard error (Cousineau, 2005).

4.4.4 Discussion

Configural priming still modulates ILs in 4-item displays although this effect is weaker than in 3-item displays: The previous distractor position does not show the same facilitation as the

previous target position. This indicates that the number of search items affects the speed at which processing progresses from global-to-local levels. With a greater number of items the global representation of the scene is generated faster hence ILs begin to be modulated by local-level biases (i.e. position priming). That MD shows no significant effect of position priming is surprising, but may suggest that target selection is resolved (i.e. the global-to-local process is complete) by the time at which MD occurs. (Also note, however, that the increased error caused by fewer target repeats may have contributed to the lack of position priming effect on MD; see Fig. 4.8, panel A, left).

4.5 General discussion

The aim of this chapter was to investigate whether the global-to-local cascade of visual information processing leaks into reaching movements. Indeed, three experiments showed that the configuration of the items (global-level), and not the target/distractor positions, influenced the time at which the reach was initiated. The target position (local-level) affected the reaching trajectories themselves (i.e. the later movement phase). These effects were measured in terms of configural and position priming.

Moreover, configural priming effects on IL showed little sensitivity to changes in repetition probability. Conversely the effect of position priming on MD was strongly affected by a change in repetition probability. Interestingly, sensitivity to changes in priming probability is often interpreted as an indication that a process is top-down modulable rather than being driven purely by bottom-up computation (see Geyer & Müller, 2009; Thomson, D'Ascenzo, & Milliken, 2013; for detailed discussions). Thus, the present results suggest that configural perception, unaffected by repetition probability, is under bottom-up control. In contrast, local-level processes, such as position priming appear to be top-down modulable.

These conclusions are consistent with predictions from Hochstein & Ahissar's (2002) reverse hierarchy theory (RHT). They suggested that local-level processing is guided by the outcome of global-level processing via a "re-entry" process (top-down control). In contrast, global-level processing is assumed to be driven in a bottom-up fashion.

The results of Experiment 4.4 suggest that the number of display items can influence the speed with which processing progresses from global-to-local representations. This is in accordance with research showing that numerosity processing of visual stimuli relies on rapid, parallel processes (e.g. Utochkin, 2013). Furthermore such set size effects can also be explained by RHT (Hochstein & Ahissar, 2002) whereby progress through an implicit forward hierarchy is speeded by increasing the number of items (possibly due to greater contrast/salience, e.g. Sagi & Julesz, 1987; promoting perceptual grouping, e.g. Bravo & Nakayama, 1992). This gives a faster representation of global-level properties. It then allows for earlier re-entry into local-level processing that begins to modulate reach ILs. By the time at which MD occurs both forward and re-entrant sweeps through the hierarchy have been completed meaning position priming effects are reduced.

In a broader sense, these findings demonstrate that whilst sensitive to dynamic target selection biases, the CRT measures themselves are relatively static. Thus, IL and MD flexibly represent whichever cognitive processes happen to be ongoing at particular time points and this can differ depending on task requirements (e.g. when localising a target amongst two or three distractors). This is discussed further in 7.3.1.

It is worth noting that the influence of configuration on position priming has been highlighted in a series of RT studies by Müller and colleagues (e.g. Geyer, Müller, & Krummenacher, 2007; Geyer, Zehetleitner, & Müller, 2010). In particular, Gokce, Müller, and Geyer (2013) showed that position priming effects were strongest when the search

configuration repeated; if the configuration changed the priming effect was diminished. Gokce et al. (2013) interpreted their results as evidence for a priming memory storing not only the position of the target on the previous trial but also the configuration in which the target was embedded. When both the position and configuration in memory match the current display RTs are faster than when there is a mismatch. Combining our evidence with their explanation we can speculate that this matching process is realised by the brain in a serial fashion, i.e. configuration is matched then the position is determined. In turn, this suggests that the primary role of configural processing is to guide attention to the potential target locations. Within this framework the results are consistent with a hierarchical expectancy model (e.g. Kingstone & Klein, 1991) whereby repetition of the configuration leads to activation of the target location previously occupied within that configuration. As such, the reach trajectory deviates towards this location producing the positional priming pattern (i.e. straight reaches when the location is repeated and curved when it has switched). Such guidance of low-level search by high-level gist is central to RHT (Hochstein & Ahissar, 2002) and, in an adaptive sense, enables appropriate search for typical items (e.g. food, predators) found within a wider context. Similarly, Torralba, Oliva and colleagues (Ehinger, Hidalgo-Sotelo, Torralba, & Oliva, 2009; Oliva & Torralba, 2007; Torralba, Oliva, Castelhano, & Henderson, 2006) have demonstrated how global context guides search for local elements in real world scenes. For instance, the location of eye fixations can be predicted by the global context – e.g. towards the bottom of the display when asked to search for people in a street scene (Ehinger et al., 2009).

Rather than specifying global configural priming, an alternative explanation of the IL results can be proposed based solely on local level position processing. This would state that the previous empty locations are processed by the same local mechanisms as those that

process target and distractor locations. According to this theory, the reason it takes longer to initiate a reach to a target at a previous empty location is because there was neither positive nor negative activation on the previous trial. In other words, even when a distractor was present at the target location on the previous trial it still elicited some local level processing. This is in accordance with Tsal and Makovski's (2006) 'attentional white bear' phenomenon whereby participants are unable to ignore a distracting item – initially attending to it before subsequent suppression (see also, Humphreys, Stalmann, & Olivers, 2004; for converging evidence). This processing prompts faster selection of the target at a previous distractor location compared to when there was no local stimulus present at all (i.e. the empty condition). In effect, the starting point for achieving the activation threshold is higher for previous target and distractor locations than it is for previous empty locations, hence the local selection of a target at a previous empty location takes longer. When the distractor reaches the threshold the movement needs correcting and MD increases, producing the position priming pattern. To test this alternative explanation the limits of local processing need to be breached. A recent investigation has shown that there is a limit (approximately 6) of how many prior stimulus locations can be held in short-term memory in order to guide subsequent performance (Close, Sapir, Burnett, & d'Avossa, 2014). If the number of possible stimulus positions was increased beyond this limit then it would be impossible to use local attention to mark all previous empty and distractor locations. If the previous empty location still shows longest ILs then it would be reasonable to assume that this is due to the priming of the global configuration rather than local processing. Our design for future research will attempt to resolve this issue (see 7.5).

Yet another explanation of the IL results might argue for intact target facilitation and a lack of distractor inhibition (e.g. Fig. 4.7b). Some support for this notion is given by Geyer et

al. (2007) who showed distractor inhibition only emerged after extended practice (>1000 trials) on a target discrimination task. The main counter-argument against this point is that we already see distractor inhibition in the MD results, suggesting strongly that the selection process is sensitive to both facilitatory and inhibitory position biases from the outset.

Further efforts are needed to clarify whether the CRT still yields configural effects when there are multiple possible configurations (it may be that the value attached to representing global-level information is minimised when the number of potential configurations increases), or when the search items form irregularly spaced configurations. One might predict irregularly spaced configurations to be encoded in the same manner based on research showing configural processing of inherently 'irregular' faces (e.g. Maurer et al., 2002).

Future research could also use the CRT to examine other characteristics of global-to-local processing. To fully understand the merits of the CRT we have to re-visit an important issue with Navon's (1977) classic compound letters paradigm (see Kimchi, 1992; for a review). In Navon's procedure participants are asked to report the local letter in one block of trials and the global letter in another block. Hence the procedure involves different task requirements. However there is strong evidence that a change in task requirements can lead to a change of processing strategy and can even lead to an reversal of the processing order, i.e. local-to-global processing (see Grice, Canham, Boroughs, 1983; for early evidence and Hübner & Volberg, 2005; for a detailed discussion on the influence of task requirements in Navon's procedure). The CRT constitutes a novel method to rule out such an influence by examining global and local processing without changing the task. A widely-used method devised by Schyns and Oliva (1994) has a similar objective (see Goffaux et al., 2011 for recent application). Participants are asked whether a target scene matches the high frequency-

filtered component or low frequency-filtered component of a previous stimulus. The duration that the stimulus is presented for influences the participant's response: short presentation leads to low-frequency matching, long presentation leads to high-frequency matching. However, whilst frequency-filtering may tap into coarse processing it falls short of what is theoretically suggested to form a global level, according to classic Gestalt laws (e.g. Han & Humphreys, 1999). Hence, the present findings open up the exciting prospect that the influence of Gestalt laws on the formation of global representations can be examined without the confound of task-setting.

CHAPTER 5

Top-down Modulation of Irrelevant Feature Interference

5.0.1 Abstract

This series of experiments examined the effects of irrelevant features (IFs) on the target selection process. IFs are items that differ along a non-target-defining dimension, for instance, a large item in an odd-colour search task. Specifically, the present studies investigated the ability of an IF to capture attention under different levels of top-down control. In Experiment 5.1 target colour remained constant allowing observers to engage feature search mode. No IF interference was observed on either initiation latency (IL) or maximum deviation (MD), regardless of how unpredictable the presence of the IF was (IF predictability). In Experiment 5.2.1 target colour was randomised necessitating the engagement of singleton detection mode. Here, the observer selects the 'most different' item in the display, which allows scope for attentional capture to occur. Again, the predictability of the IF was also manipulated. Attentional capture by the IF was observed on MD (not IL), but only when the IF was unpredictable. Finally, Experiment 5.2.2 presented participants with 4 blocks of unpredictable IF trials rather than the one block presented in the previous experiments. With the greater power provided both IL and MD were modulated by the presence of the IF. These results fit with a hierarchical account of attentional control combining search modes and dimension-weighting accounts where capture occurs when in singleton detection mode and with no incentive to shift weight to the target-defining dimension.

5.0.2 Introduction

It is rare that items in our visual environment differ along only one dimension. It is much more likely that our target can be distinguished not just by colour, for example, but also by size, shape, orientation etc. Research using visual search paradigms has begun to explore the impact of irrelevant features (IFs) on our ability to select a target. The term IF refers to a

search item that differs to the other search items along a non-target-defining dimension. For instance, in a typical experiment a participant is asked to search for a green diamond amongst green circle distractors, responding according to a feature of the target shape (e.g. Theeuwes, 1992). Importantly, one of the circular distractors is also a different colour to the rest of the search items (i.e. the IF). The time taken to discriminate the target feature is often increased by the presence of the IF.

Research into IFs demonstrates the competition between top-down and bottom-up search mechanisms. In the above example, the colour of the items is irrelevant for solving the task at hand. Hence, a useful top-down strategy would restrict our search to items defined along the shape and not the colour dimension (encapsulated in the 'contingent capture' hypothesis; Folk, Remington, & Johnston, 1992). Such 'attentional setting' would always select the item that matched the goals of the observer (e.g. Dombrowe, Donk, & Olivers, 2011; Olivers & Eimer, 2010). However, the fact that an IF can increase response times suggests that such top-down strategies are not always successful, and highlights the competition between top-down and bottom-up processes. Theeuwes (1992) showed that the impact of the IF is determined by the bottom-up contrast of the IF with the items that surround it. For instance, the colour IF may well capture attention if it is bright red but possibly not if it is a lighter shade of green (Theeuwes, 1992; see also Zehetleitner, Koch, Goschy, & Müller, 2013; for evidence that a less salient IF can capture attention). Thus we have a "tug-of-war" between top-down processes and bottom-up saliency computation, the winner of which determines the influence of the IF on search performance. Whilst there have been prominent proponents of the dominance of top-down over bottom-up factors (e.g. Folk, Remington, & Johnston, 1992; Bacon & Egeth, 1994), and vice versa (e.g. Theeuwes, Reimann, & Mortier, 2006; Schreij, Owens, & Theeuwes, 2008), the clear-cut dichotomy of

bottom-up and top-down processing has come to be outdated (Awh, Belopolsky & Theeuwes, 2012). Instead, recent research has examined the conditions that lead one mechanism to over-ride the other. In line with this trend, the current studies present the first investigation of the concurrent modulation of bottom-up IF interference by two top-down factors: the search mode employed and the predictability of the IF presence.

5.0.2.1 Search mode

Bacon and Egeth's (1994) *search modes* theory proposed two types of attentional control that can be engaged according to the task demands: feature search mode and singleton detection mode. If the target-defining feature (e.g. colour) remains the same throughout a trial block observers can use feature search mode to find the target. That is, they can set themselves for a red item and suppress all other distractors, irrespective of their dimension. However, if the target-defining feature changes unpredictably the observer is unable to search for one particular colour. In this case they engage singleton detection mode selecting the item that is most 'different' from the others. Thus, singleton detection mode allows scope for an IF to capture attention. This is supported by a raft of neurophysiological evidence showing attentional capture-related N2pc responses to an IF when in singleton detection mode but not feature search mode (e.g. Burra & Kerzel, 2013; Eimer & Kiss, 2010; Eimer, Kiss, Press, & Sauter, 2009; Kiss, Grubert, Petersen, & Eimer, 2012; Kiss & Eimer, 2011).

5.0.2.2 Irrelevant feature predictability

We also wanted to observe how the predictability of the target (and therefore the search mode engaged) interacted with the predictability of the IF. As predicted by the Dimension Weighting Account (DWA; Müller, Heller, & Ziegler, 1995; Müller, Reimann, &

Krummenacher, 2003; see 1.6.5), IFs that appear on a large proportion of trials, and are thus more predictable, have been shown to capture attention less than rarely presented IFs (Geyer, Müller, & Krummenacher, 2008; Müller, Geyer, Zehetleitner, & Krummenacher, 2009). As the presence of an IF becomes more frequent there is an incentive to suppress it meaning weight shifts towards the target-defining dimension thereby reducing attentional capture. However, investigations into the effects of IF predictability have thus far only examined performance when feature search mode is engaged (e.g. Geyer et al., 2008; Müller et al., 2009), and even then results are somewhat inconsistent. For instance, Noesen, Lien, and Ruthruff (2014) found no attentional capture by abrupt onset IFs even when their presence was particularly rare (10% of trials).

5.0.2.3 The present studies

In isolation both the search mode employed and the weight attached to the target/IF dimensions have been shown to modulate IF interference. To the author's knowledge no study has yet examined the relative importance of these top-down factors for overcoming attentional capture. This was the goal of Chapter 5.

To this end the present studies will vary both the predictability of the target colour and the predictability of the IF presence, and examine the resultant IF interference. If the deployed search mode is the main determinant of IF capture then the IF should not disrupt search when feature search mode is engaged, irrespective of the weight attached to the target/IF dimensions (i.e. the IF predictability). This would be in accordance with Noesen et al. (2014) who showed no interference by a rarely presented IF in feature search mode, but would be inconsistent with Geyer et al. (2008) and Müller et al. (2009). Conversely, if the weight attached to the target/IF dimensions is the main determinant of IF interference then the IF may

capture attention irrespective of the search mode employed. Here, an unpredictable IF would interfere with search even when the target colour is predictable. This would be in accordance with Geyer et al. (2008) and Müller et al (2009), but would be inconsistent with Noesen et al. (2014). These contrasting predictions were tested in Experiment 5.1.

Bacon and Egeth (1994) argue that capture should only occur when in singleton detection mode. Hence, IF interference should be observed in Experiment 5.2.1 where the target colour is unpredictable. As yet it is unknown whether the predictability of the IF modulates attentional capture when singleton detection mode is engaged. Since Geyer et al. (2008) and Müller et al. (2009) observed capture by a rarely presented IF in feature search mode we might also predict capture in singleton detection mode where less top-down control is available. Whether a predictable IF captures attention when singleton detection mode is engaged remains to be seen.

Finally, Theeuwes (1992) would state that bottom-up capture will occur regardless of the search mode employed and the predictability of the IF presence. The present studies represent the first attempt to investigate the combined effects of target predictability and IF predictability to overcome such attentional capture.

5.0.2.4 Time course of bottom-up and top-down influences

On a broader level the present experiments will use the CRT to test the notion that bottom-up saliency processing always precedes top-down, goal-driven control (see Theeuwes, 2010; for a review). Chapter 4 introduced Reverse Hierarchies Theory (RHT) as a framework for the flow of visual information through the brain (see 4.5). The initial, feedforward sweep through the hierarchy is rapid and based on bottom-up computation before deliberate, top-down re-entry occurs. Theeuwes (2010) argument for the compulsory precedence of bottom-up

processes follows a similar rationale. He states that the shift in spatial attention to the region with the highest salience is based purely on bottom-up computation and is immune from the goals or strategy of the observer. At a later time point, and only if attention has been misguided (i.e. directed to an IF rather than the target), top-down control is recruited to re-orient attention to the target. Theeuwes acknowledges top-down control plays a role in task completion but argues that initial attentional selection is purely bottom-up. Theeuwes (2010) draws much behavioural and neurophysiological evidence in support of this theory. For example, Theeuwes (1992, 1994) initial experiments (see 1.6.3) showed that even when the IF is present on 100% of trials and the target feature remains constant attention is still captured by the IF. Furthermore, this capture is modulated by saliency and is unaffected by extended practice, suggesting reliance on bottom-up computation. These behavioural results have been replicated and extended on numerous occasions (e.g. Lu & Han, 2009; Mounts, 2000; Pinto, Olivers, & Theeuwes, 2005; Schubö, 2009). Kim and Cave (1999) combined Theeuwes (1992) paradigm with a probe detection task where a probe is presented at the previous location of a target or distractor at variable stimulus onset asynchronies (SOA). They showed that if the probe is presented at a previous distractor IF location at 60ms SOA detection was faster than when it was presented at the target location. Conversely, with a 150ms SOA probe detection was faster at the target versus distractor IF locations. This supports the claim that initially (i.e. approximately 60ms) attention is captured automatically before being re-directed to the target by top-down processes.

Neurophysiological evidence for the primacy of bottom-up processes stems from ERP, and single-cell recording studies. Hickey, McDonald, and Theeuwes (2006) showed that the N2pc occurred first in the hemisphere contralateral to an IF singleton, prior to the N2pc in the contralateral target hemisphere suggesting that the IF was attended prior to the target (see

also, Kiss, Van Velzen, & Eimer, 2008; Schubö, 2009). Ogawa and Komatsu (2004) recorded activity from single-cells in monkey V4 whilst they completed either a shape or colour search task. The researchers manipulated the property of the search item that fell within the receptive field (RF) of the particular neuron. Regardless of whether the monkey was searching for a colour- or shape-defined target the firing rate remained the same up until 175ms post-onset. After 175ms the neuron's firing rate is modulated by the task-relevance of the item within its RF – maintaining an increase if it matches the target dimension or showing reduced firing if the item is an IF. Again, this is evidence for the initial sweep of information through the brain being completely bottom-up before top-down biases are able to take effect (in this case after 175ms).

Counterarguments to Theeuwes (2010) theory were summarised in Egeth, Leonard, and Leber (2010). Of particular relevance are ERP studies overlooked by Theeuwes (2010) that indicate early activity is influenced by attentional setting. For instance, Zhang and Luck (2009) asked participants to track the motion of target-colour dots around the periphery of an attended visual field. On certain trials an irrelevant set of dots appeared in the opposite visual field. Results showed that the irrelevant dots modulated early activity (approximately 100ms after presentation), but only if they matched the colour of the attended dots. This suggests that the observers attentional set is able to influence rapid processing and supports the notion that attentional capture can be prevented from the outset of each trial without the need for delayed top-down re-entry. Furthermore, there is also evidence that neural activity can be modulated by attentional-setting prior to stimulus presentation (e.g. in area V4; Hayden & Gallant, 2005). This shift in baseline activity due to the adoption of a particular search strategy is clearly incompatible with Theeuwes (2010) view of compulsory bottom-up precedence (see

Ansorge, Kiss, Worschech, & Eimer, 2011; for further evidence for early and enduring effects of top-down modulation).

To challenge Theeuwes (2010) notion using a behavioural technique evidence of top-down modulation on early processing would need to be demonstrated, rather than top-down modulation from recurrent connections. With regards to the present experiments this would mean suppression of attentional capture effects on IL as well as MD. Whether this lack of attentional capture is due to the participant's search mode or due to the weight attached to the target-defining dimension should be made clear by the results of Experiments 5.1 and 5.2.1.

Experiment 5.1: Effects of IF Predictability on Feature Search Mode

5.1.1 Introduction

The first two studies presented in this chapter investigated the interaction between the attentional strategy employed (i.e. feature search mode versus singleton detection mode) and the top-down influence of IF predictability using the CRT. The displays used throughout this chapter are illustrated in Fig. 5.1. Experiment 5.1 asked participants to reach and touch the same colour target on every trial. In line with Bacon and Egeth (1994) the observer should enter into feature search mode. If search mode is the primary determinant of attentional capture then IF interference from the distractor IF in Fig. 5.1B should be eradicated, regardless of IF predictability (consistent with Noesen et al., 2014). Conversely, if the weight attached to the target/IF dimensions still contributes to target selection then an unpredictable IF should capture attention even when feature search mode is engaged (consistent with Geyer et al., 2008; Müller et al., 2009). Finally, Theeuwes (1992) would predict capture regardless of the target/IF predictability.

Theeuwes (2010) and Egeth et al. (2010) offer divergent predictions about the locus of IF interference. If Theeuwes (2010) is correct IL should show attentional capture by the IF since early influences of the IF are immune to top-down suppression. The MD is unlikely to show capture because by this point top-down biases can take effect. On the other hand Egeth et al. (2010) argue that early processing is subject to attentional control (see also, Ansorge et al., 2011; Zhang & Luck, 2009). Thus, null effects of the IF would be predicted on both IL and MD.

5.1.2 Method

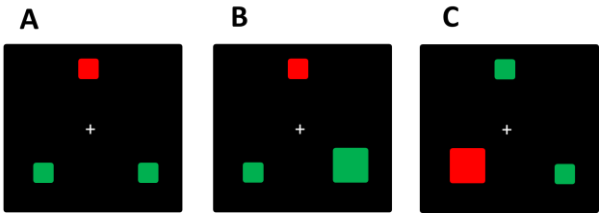

Fig. 5.1. Illustration of the three IFCondition trials used in the present experiment (A = no IF, B = distractor IF, C = target IF). In Experiment 5.1 target colour remained constant throughout (i.e. the red square in this example) but changed unpredictably from trial-to-trial in Experiments 5.2.1 and 5.2.2.

The method matched that of Experiment 2.1 with the following exceptions.

Participants. Ten participants (four male) aged 18-25 (mean 19.7) were recruited from the student population at the University of Birmingham. All were right-handed with normal or corrected-to-normal visual acuity and normal colour vision.

Stimuli. All trials were 3-item odd-colour search trials. On trials with an IF present one of the squares was larger than the other two (5.7° x 5.7° versus 3.8° x 3.8°).

Design. Participants completed four blocks of 96 trials. Fig. 5.1 illustrates the different display types. Three of the four blocks were predictable IF blocks and one was an unpredictable IF block. In the first predictable IF block the IF was absent (no IF); hence all trials had three normal sized stimuli (Fig. 5.1A). In the second predictable block the IF coincided with the distractor on 100% of trials (distractor IF; Fig. 5.1B); in the third block the IF coincided with the target on 100% of trials (target IF; Fig. 5.1C). Finally, in the unpredictable block the previous 3 trial types were equally but randomly intermixed. Thus 33% of the trials were no IF, 33% were target IF, and 33% were distractor IF. Importantly target colour (red/green) was chosen randomly for the first trial of each block and remained the same throughout that block of trials (i.e. predictable target). Block order was counterbalanced across participants.

Dependent variables were IL and MD. To examine the effects of IF predictability a two-way within-subjects ANOVA was conducted with factors IFCondition (no IF, target IF, distractor IF) and IFPredictability (predictable vs. unpredictable; i.e. performance in the no IF, target IF, and distractor IF blocks compared to the respective 33% of trials in the unpredictable IF block). Paired-samples t-tests investigated any significant main effects. Where appropriate simple effects analyses compared IF Conditions separately for predictable IF and unpredictable IF trials.

5.1.3 Results

Before conducting the analysis error trials and outliers were removed. This resulted in 6.1% of trials being discarded (3.4% outliers with IL>2 standard deviations from mean per participant; 2.7% motion capture errors). 2.5% of the motion capture errors stemmed from

one block of trials which failed to record (predictable no IF condition). The remaining blocks of trials from this participant were still analysed.

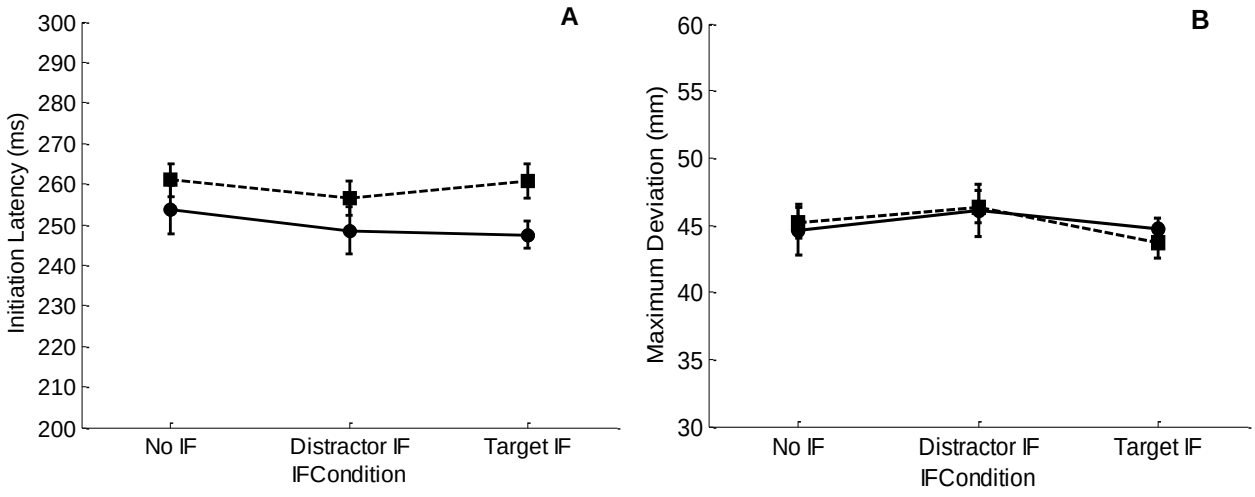

Fig. 5.2. The effects of IFPredictability on initiation latency (A) and maximum deviation (B) according to IFCondition in Experiment 5.1. Solid line represents the predictable IF condition, dashed line represents the unpredictable IF condition. Error bars reflect within-subjects standard error (Cousineau, 2005).

Performance on predictable IF and unpredictable IF trials according to IFCondition are shown in Fig. 5.2. There was no main effect of IFCondition ($F(2,16)=0.20$, $p>0.250$, $\eta_p^2=0.02$) or IFPredictability ($F(1,8)=1.74$, $p=0.22$, $\eta_p^2=0.18$) on IL or any significant interaction ($F(2,16)=0.26$, $p>0.250$, $\eta_p^2=0.03$). MD results showed the same pattern: there was no effect of IFCondition ($F(2,16)=0.81$, $p>0.250$, $\eta_p^2=0.09$) or IFPredictability ($F(1,8)=0.01$, $p>0.250$, $\eta_p^2=0.001$) and no interaction ($F(2,16)=0.12$, $p>0.250$, $\eta_p^2=0.02$).

5.1.4 Discussion

Results from Experiment 5.1 showed no influence of IFs on either IL or MD. Hence, when the participant can engage feature search mode an IF fails to capture attention regardless of its predictability. These findings support Bacon and Egeth (1994) and argue against Theeuwes (1992) attentional capture hypothesis. They are also consistent with ERP findings showing that an IF fails to elicit an N2pc component (i.e. capture attention) when the target identity remains the same across trials (e.g. Eimer & Kiss, 2010; Kiss & Eimer, 2011). Interestingly, the lack of attentional capture by the IF is in spite of the fact that here the IF could coincide with the target, and thus should be more likely to capture attention than in Theeuwes (1992) where the IF always coincided with a distractor (see Proulx, 2010).

However, the results are inconsistent with Geyer et al. (2008) and Müller et al. (2009) who demonstrated capture by a rare IF in feature search mode (again this is despite the IF never coinciding with the target in either Geyer et al. or Müller et al.). The results suggest that the search mode employed is of greater importance than the weight attached to the target/IF dimensions: When feature search mode is engaged (un)predictability of the IF is irrelevant. Finally, although Theeuwes (2010) would have predicted the lack of MD effect (since top-down biases can suppress the IF by this point), his theory would have predicted an influence of the IF on IL. Thus, the results from Experiment 5.1 argue against the compulsory precedence of bottom-up computation over top-down control, instead suggesting that attentional set impacts early, feedforward processing.

Experiment 5.2.1: Effects of IF Predictability on Singleton Detection Mode

5.2.1.1 Introduction

Experiment 5.2 replicated the design of Experiment 5.1 but with target colour free to vary randomly. This should result in participants engaging singleton detection mode and therefore increase the chances of attentional capture by the distractor IF (Bacon and Egeth, 1994; Eimer & Kiss, 2010). Again, predictability of the IF was also varied to examine, for the first time, whether performance in singleton detection mode is susceptible to modulation by the weight attached to the target/IF dimensions, unlike feature search mode (Experiment 5.1).

5.2.1.2 Method

The method matched that of Experiment 5.1 with the following exceptions.

Participants. 13 participants (five male) aged 19-37 (mean 26.9) were recruited from the University of Birmingham.

Design. Participants completed the same 4 blocks of 96 trials but the target colour was selected randomly on each trial (whilst still maintaining a 50-50 split of red and green targets). Analyses were extended to include a between-experiments comparison of Experiment 5.1 (predictable target) and Experiment 5.2.1 (unpredictable target). Thus experiment was added as a factor in an additional 3-way ANOVA.

5.2.1.3 Results

Prior to analysis error trials and outliers were removed. This resulted in 5.1% of trials being discarded (4.0% outliers, 1.1% motion capture errors). The effects of IFCondition and IFPredictability are shown in Fig. 5.3.

Initiation latency. The effect of IFCondition on IL approached significance ($F(2,24)=2.76$, $p=0.08$, $\eta_p^2=0.19$). ILs were also influenced by IFPredictability ($F(1,12)=13.94$, $p=0.003$, $\eta_p^2=0.54$) with predictable IF trials exhibiting shorter ILs than unpredictable IF trials (300ms

vs. 325ms). Importantly, there was a significant IFCondition x IFPredictability interaction ($F(2,24)=5.68$, $p=0.01$, $\eta_p^2=0.32$). This was driven by a significant reduction in performance when the IF was unpredictable for the distractor IF ($t(12)=2.31$, $p=0.04$) and target IF conditions ($t(12)=5.39$, $p<0.001$) whereas the no IF condition showed no effect of predictability ($t(12)=0.83$, $p>0.250$; compare dashed and solid lines at three IFConditions in Fig. 5.3A).

The IFCondition x IFPredictability interaction was further examined via simple effects analyses. Firstly, comparing performance in the predictable IF conditions (i.e. solid line, Fig. 5.3A) resulted in an effect of IFCondition on IL ($F(2,24)=6.42$, $p=0.006$, $\eta_p^2=0.35$). This was driven by a shorter IL on target IF trials compared to distractor IF ($t(12)=2.79$, $p=0.02$) and no IF trials ($t(12)=3.19$, $p=0.008$). There was no difference in ILs across unpredictable IF conditions (i.e. dashed line, Fig. 5.3A; $F(2,24)=1.06$, $p>0.250$, $\eta_p^2=0.08$).

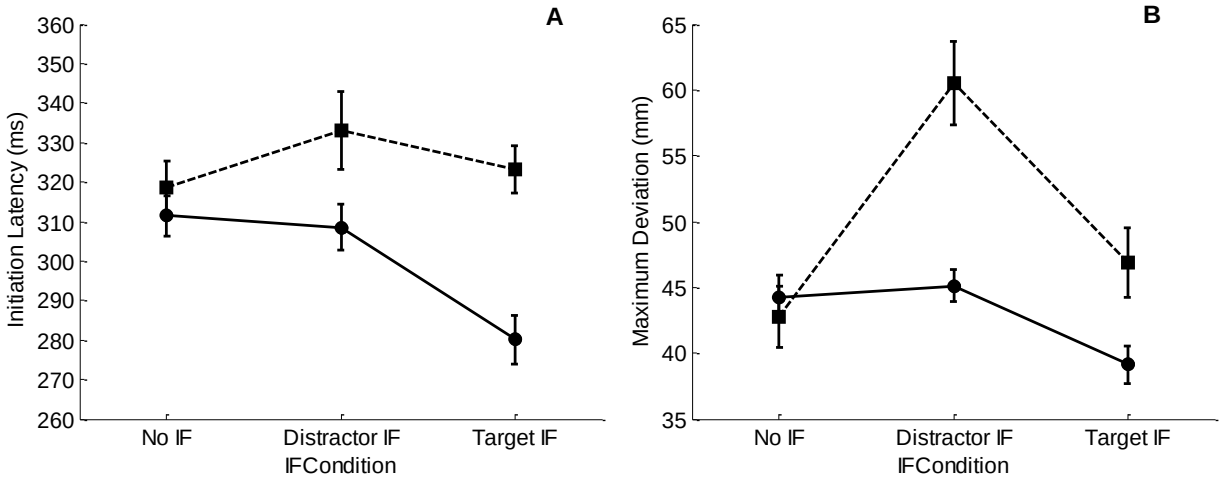

Fig. 5.3. The effects of IFPredictability on initiation latency (A) and maximum deviation (B) in Experiment 5.2.1. Solid line represents the predictable IF condition, dashed line represents the unpredictable IF condition. Error bars reflect within-subjects standard error (Cousineau, 2005).

Maximum deviation. There was a significant main effect of IFCondition on MD ($F(2,24)=21.36$, $p<0.001$, $\eta_p^2=0.64$). MD was also affected by IFPredictability ($F(1,12)=7.97$, $p=0.02$, $\eta_p^2=0.40$). Similar to the IL results reported above predictable IF trials showed less deviation than unpredictable IF trials (42.82mm vs. 50.06mm). There was a significant IFCondition x IFPredictability interaction ($F(2,24)=6.62$, $p=0.005$, $\eta_p^2=0.36$). Again the no IF trials were unaffected by predictability ($t(12)=0.40$, $p>0.250$). However, unpredictable distractor IF trials were more curved than predictable distractor IF trials ($t(12)=4.10$, $p=0.001$), with a borderline increase from unpredictable target IF trials to predictable target IF trials ($t(12)=2.07$, $p=0.06$).

A simple effects analysis revealed significant differences between predictable IF conditions (i.e. solid line, Fig. 5.3B; $F(2,24)=4.02$, $p=0.03$, $\eta_p^2=0.25$). The target IF condition showed the best performance with less deviation than distractor ($t(12)=2.52$, $p=0.03$) and no IF trials ($t(12)=2.51$, $p=0.03$). Importantly, there were also differences in MD between unpredictable IF conditions (i.e. dashed line, Fig. 5.3B; $F(2,24)=15.28$, $p<0.001$, $\eta_p^2=0.56$). Distractor IF trials showed greater deviation than both no IF ($t(12)=5.10$, $p<0.001$) and target IF trials ($t(12)=3.45$, $p=0.005$), with no difference between no IF and target IF trials ($t(12)=1.67$, $p=0.12$).

The effects of search mode. A main effect of experiment was observed on IL when it was added in a subsequent 3-way mixed ANOVA ($F(1,20)=5.55$, $p=0.029$, $\eta_p^2=0.22$). ILs in the predictable target experiment (Experiment 5.1, i.e. feature search mode) were significantly faster than in the unpredictable target experiment (Experiment 5.2.1, i.e. singleton detection mode; 257ms vs. 312ms). Experiment did not interact with either IFCondition or IFPredictability (ps>0.250).

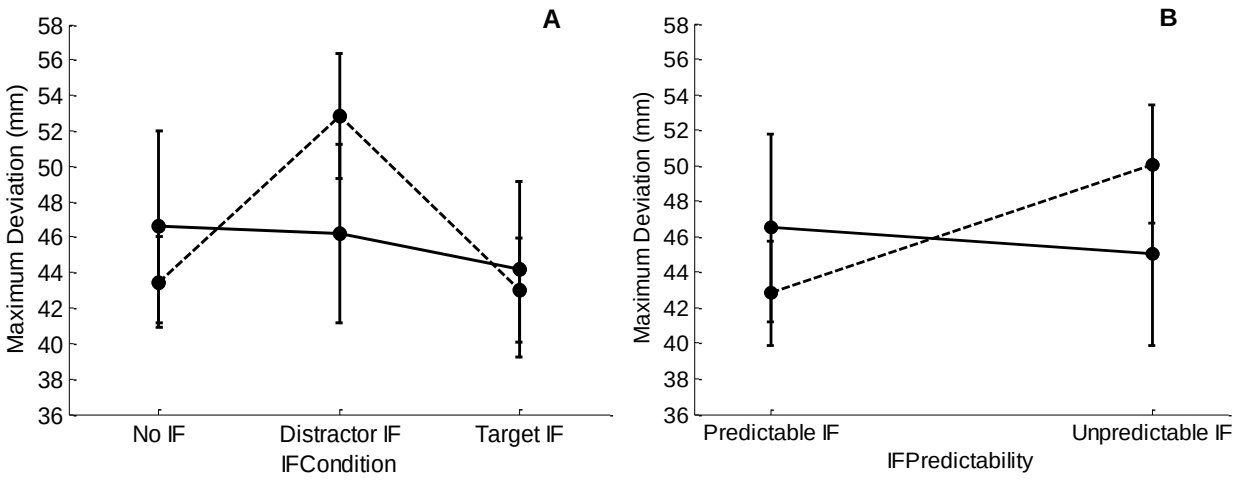

Fig. 5.4. A: Interaction between IFCondition and experiment affecting MD. B: Interaction between IFPredictability and experiment affecting MD. Solid line = predictable target (Experiment 5.1), dashed line = unpredictable target (Experiment 5.2.1). Error bars reflect between-subjects standard error.

There was no main effect of experiment on MD ($F(1,20)<0.001$, $p>0.250$, $\eta_p^2<0.001$). However, there were interactions with both IFCondition (Fig. 5.4A; $F(2,40)=8.10$, $p=0.001$, $\eta_p^2=0.29$) and IFPredictability (Fig. 5.4B; $F(1,20)=4.82$, $p=0.04$, $\eta_p^2=0.19$). To investigate the interactions two separate 2-way ANOVAs were conducted with factors experiment x IFCondition and experiment x IFPredictability. An interaction between experiment and IFCondition was observed ($F(2,40)=8.10$, $p=0.001$, $\eta_p^2=0.29$). This confirms that there was no difference between IF conditions when the target colour was predictable (solid line, Fig. 5.4A; see 5.1.3), but significantly greater MD in the distractor IF condition when the target colour was unpredictable (dashed line, Fig. 5.4A; see *Maximum deviation*, above). Thus, MD reveals attentional capture by a distractor IF when the target is unpredictable.

An interaction between experiment and IFPredictability was also observed ($F(1,20)=4.82$, $p=0.04$, $\eta_p^2=0.20$). Fig. 5.4B shows that when the target is predictable (Experiment 5.1) the presence of an IF has no effect on MD regardless of IF predictability

(solid line, Fig. 5.4B; see 5.1.3). However, the IF captures attention when both the colour of the target and the presence of the IF are unpredictable (dashed line, Fig. 5.4B; see *Maximum deviation*, above).

5.2.1.4 Discussion

Experiment 5.2.1 aimed to investigate IF interference when the participant is forced to engage singleton detection mode. The results can be summarised as follows. When using IL as the index of attention there was no attentional capture by the IF even when its presence was unpredictable. Target IF trials did exhibit shorter ILs than both distractor IF and no IF trials (Fig. 5.3A) consistent with widely reported redundancy effects (e.g. Krummenacher, Müller, & Heller, 2001), whereby an item salient along two dimensions receives increased activation. Indeed, this increased activation, even though the colour and not the size was the target-defining feature, provides confirmation that the observer had engaged singleton detection mode. Attentional capture did occur when using MD as the attentional index but only when the IF presence was unpredictable. This is shown in the increased MD for distractor IF versus no IF and target IF trials (Fig. 5.3B), and by significant interactions between experiment and IFPredictability/IFCondition for MD (Fig. 5.4). Thus, IF interference was only observed when both the target feature and the IF presence was unpredictable, i.e. when no method of top-down control could be employed.

The results indicate that when in singleton detection mode the weight attached to the target dimension in the presence of a predictable IF is adjusted to a greater extent and plays more of a role than when in feature search mode, hence, the impact of IF predictability in Experiment 5.2.1 but not in Experiment 5.1. In turn this suggests a hierarchy of 'top-down' modulation with overarching attentional set (i.e. singleton detection mode or feature search

mode) determining the influence of other top-down biases such as the weight attached to search dimensions (see 5.3, and Fig. 5.6).

The fact that attentional capture was revealed in the MD and not the IL is inconsistent with both Theeuwes' (2010) and Egeth et al.'s (2010) theories. Theeuwes (2010) would predict capture effects on IL since it is here that bottom-up influences are most prominent – if top-down modulation does occur it will affect later processing and *reduce* the IF influence on MD. Egeth et al. (2010) argue that top-down modulation is possible on early processing hence they can explain the lack of IL effect. However, they cannot explain why MD would subsequently be subject to capture when it has previously been suppressed. It is important to note that the unpredictable IF conditions comprised only one block of trials in Experiment 5.2.1. It may be with more power we do see effects of the unpredictable IF on IL. Experiment 5.2.2 will investigate this by presenting participants with 4 blocks of unpredictable IF trials.

Experiment 5.2.2: Effects of an Unpredictable IF on Singleton Detection Mode

5.2.2.1 Introduction

Experiment 5.2.2 was conducted to determine whether a lack of power caused by the low number of trials in the unpredictable IF condition of Experiment 5.2.1 caused the absence of IF interference on ILs. If IF interference is observed on both IL and MD it would support a compromise between the theories of Theeuwes (2010) and Egeth et al. (2010): attentional capture can influence the entire selection process but only when observers are engaged in singleton detection mode and the IF presence is unpredictable.

5.2.2.2. Method

The method matched that of Experiment 5.1 with the following exceptions.

Participants. 13 participants (three male) aged 18-22 (mean 19.4) were recruited from the student population at the University of Birmingham.

Design. Participants completed 4 blocks of 96 trials. There were no predictable IF conditions. Hence, every block was an unpredictable IF block comprised of 33% no IF trials, 33% distractor IF trials, and 33% target IF trials. Target colour was randomly selected on each trial. IL and MD were analysed using a one-way within-subjects ANOVA with unpredictable IF condition (no IF, distractor IF, target IF) as the sole factor.

5.2.2.3 Results

Outliers were removed prior to analysis. This resulted in 5.2% of trials being discarded (3.5% outliers, 1.7% motion capture errors).

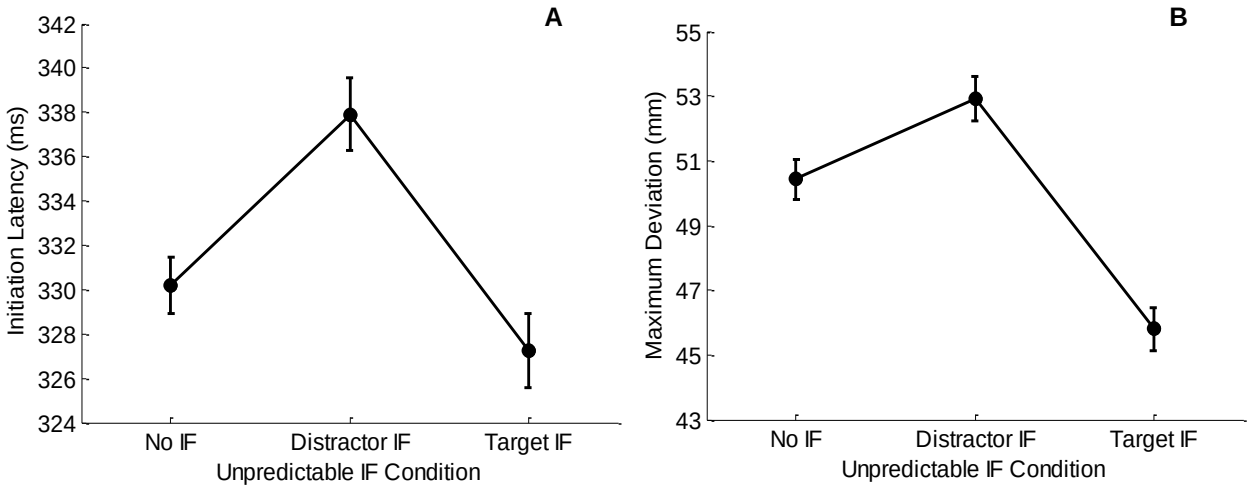

Fig. 5.5. Effects of an unpredictable IF on initiation latency (A) and maximum deviation (B) in Experiment 5.2.2 Error bars reflect within-subjects standard error (Cousineau, 2005).

There was a significant main effect of unpredictable IF on IL ($F(2,24)=8.56$, $p=0.002$, $\eta^2=0.42$; Fig. 5.5A). Distractor IF trials started later than both no IF ($t(12)=3.18$, $p=0.008$) and target IF trials ($t(12)=3.47$, $p=0.005$). There was no difference in IL between no IF and target IF trials ($t(12)=1.20$, $p=0.25$). A main effect of unpredictable IF on MD was also observed ($F(2,24)=20.24$, $p<0.001$, $\eta^2=0.63$; Fig. 5.5B). Significant differences existed between all three unpredictable IF conditions: Distractor IF trials exhibited greater curvature than both no IF ($t(12)=2.24$, $p=0.045$) and target IF ($t(12)=5.87$, $p<0.001$) trials, whilst target IF trials were also less curved than no IF trials ($t(12)=4.29$, $p=0.001$).

5.2.2.4 Discussion

The results of Experiment 5.2.2 show that with enough power IF interference is observed on both IL and MD when the participant is engaged in singleton detection mode and the presence of the IF is unpredictable. Thus, attentional capture occurs when no top-down control is available. Due to the lack of early or late top-down biases this capture influences the entire selection process, modulating both IL and MD.

5.3 General discussion

The results from the three experiments presented here suggest that attentional capture occurs when the observer is forced to engage singleton detection mode and top-down weight cannot be shifted to the target dimension due to IF unpredictability. Under these circumstances both early and late indices of selection are affected by a distracting IF. Where the participant is able to engage feature search mode, or when predictability provides an incentive to suppress the IF in singleton detection mode, attentional capture does not occur.

The theoretical viewpoints of Theeuwes (2010) and Egeth and colleagues (2010) can be summarised as follows. Theeuwes argued for attentional capture by salient items occurring on the feedforward sweep of information through the brain that is impenetrable by top-down biases. Hence, IF capture should modulate early indices of attention but top-down influences may reduce the impact on later processing. Conversely, Egeth et al. stated that even the earliest processing is subject to top-down modulation in the form of attentional setting that causes baseline shifts in neural activity (e.g. Chawla, Rees, & Friston, 1999; Zhang & Luck, 2009). The results of the present studies lend support to Egeth et al.'s theory of early and continuous top-down control, with capture only occurring when any form of top-down control (i.e. either attentional set or dimension weighting) is impossible.

The primary evidence for early top-down modulation of attentional capture is provided by Experiment 5.1. Enabling the observer to engage feature search mode by maintaining the same target colour meant the IF failed to capture attention. This was the case when examining both IL and MD suggesting the attentional set of the observer impacts early processing, in line with Egeth et al. (2010), and recent ERP evidence (e.g. Eimer & Kiss, 2010; Kiss & Eimer, 2011). Based solely on the results from Experiment 5.1 it could be argued that IL occurs too late to reveal feedforward attentional capture (see Belopolsky, Schreij, & Theeuews, 2010; for the first to make this point). However, when viewed alongside the results of Experiment 5.2.2 we see that ILs were in fact 80ms slower in Experiment 5.2.2 yet capture was still observed. This implies that IL is able to index early biases in a similar manner to that shown in Chapter 4 where early and late processes were dissociated using IL and MD.

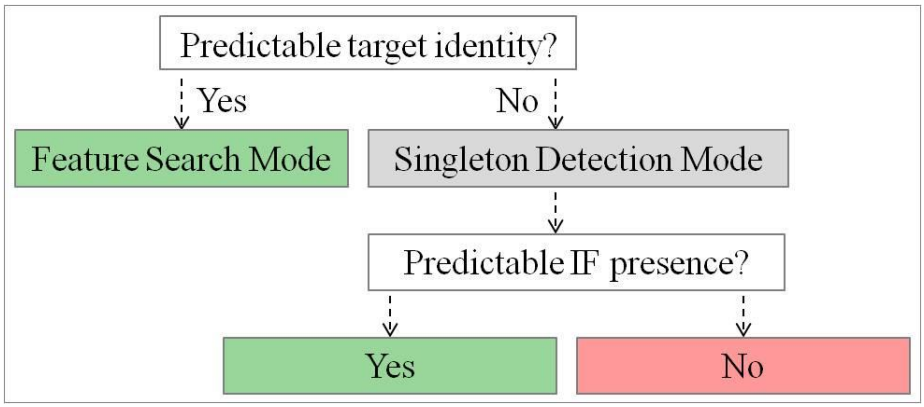

Fig. 5.6. Hierarchy of top-down control that determines whether or not an irrelevant feature (IF) captures attention based on the results of the present experiments. Green = no attentional capture, red = attentional capture.

When forced to engage singleton detection mode in Experiments 5.2.1 and 5.2.2 the IF did capture attention but only when there was no motivation to use another top-down bias – the predictability of the IF presence. Until now research has focused on the isolated top-down influences of search mode (e.g. Eimer & Kiss, 2010) and dimensional weight (e.g. Geyer et al., 2008) on IF capture. By examining their combined effects our results indicate a hierarchy of top-down influence. This hierarchy is illustrated in Fig. 5.6. Firstly, the search mode of the observer is the primary determinant of attentional capture. If feature search mode is deployed, no capture will occur. Consistent with Guided Search (Wolfe, 1994), foreknowledge of the target identity may cause a baseline shift in activity that biases not only re-entrant but also rapid feedforward selection decisions in favour of that colour (e.g. Chawla et al., 1999; Hayden & Gallant, 2005; Zhang & Luck, 2009). Only when singleton detection mode is engaged does control shift to the next level of the hierarchy. The overarching importance of search mode compared to IF predictability is consistent with previous studies showing that an

unpredictable IF fails to capture attention when feature search mode is engaged (e.g. Noesen, et al., 2014; Yantis & Egeth, 1999), yet is inconsistent with other findings of IF predictability modulation in feature search mode (Geyer et al., 2008; Müller et al., 2009). One reason for this discrepancy is that the studies of Geyer et al. and Müller et al. present the IF on a lower proportion of trials than the current studies meaning their IF was more unpredictable and may have disrupted performance despite the deployment of feature search mode. Here the IF is present on 66% of trials (although, only coincides with the distractor on 33%) whereas the prior studies presented the IF on as few as 20% of trials. However, in the present studies the IF was as likely to coincide with the target as the distractor whereas Geyer et al. and Müller et al. used an additional singleton paradigm where the IF could only coincide with a distractor. Thus, because in the present studies the IF could provide target-relevant information it should not have been totally suppressed. This should offset the IF being present in a greater proportion of trials compared to Geyer et al. and Müller et al.'s studies and result in similar capture effects. The present results are also in accordance with Bacon and Egeth's (1994) original formulation of feature search mode that assumes overall top-down control of IF attentional capture.

For the first time we have shown that the weight attached to the target/IF dimensions modulates capture in singleton detection mode: If the IF appears consistently across trials weight is shifted towards the target-defining dimension and interference is reduced (cf. Müller et al., 1995, 2003; see 1.6.5). If the IF is unpredictable weight remains centrally distributed between target and IF dimensions. Under these conditions of maximum unpredictability the IF captures attention and the effects can be seen on both early and late indices of attention.

CHAPTER 6

Guidance of Search by an Irrelevant Feature

6.0.1 Abstract

The present chapter examined the impact of an IF coinciding with multiple items on search performance. Specifically we tested whether grouping promoted by the size of the search items influenced search. In Experiment 6.1 participants performed a compound key-press task identifying a letter embedded within an odd-colour target. On each trial the target could be large (T) or small (t) and the distractors could be either both small (dd), both large (DD), or of different sizes (Dd), thus producing a factorial combination of IF presence and coincidence. Reaction times (RTs) were fastest when the IF promoted proximity grouping of the distractors. RTs were also modulated by similarity grouping with worst performance when the distractors were different sizes and the large target was grouped by proximity to a distractor (TDd). Using the CRT, Experiment 6.2.1 showed that distractor proximity grouping had early (IL) and enduring effects (MD) on selection whereas distractor similarity effects were restricted to MD. A control experiment indicated that the combined effects of proximity and similarity grouping on MD in Experiment 6.2.1 may have been revealed were it not for underlying motor-related differences in reaching to large and small targets. For the first time, the results showed how multiple IF items modulate search performance by promoting perceptual grouping and demonstrated the time course of grouping processes using a behavioural technique.

6.0.2 Introduction

The studies discussed in Chapter 5 focused on the disruption of search performance caused when an IF coincides with a single search item. This chapter extends the investigation of search performance in the presence of an IF to situations where the IF can coincide with

multiple search items. This enables us to use the IF methodology to examine the influence of perceptual grouping on search performance.

Target selection is facilitated if the target can be segmented from the distractors and the distractors can be grouped together. This is encapsulated within Duncan and Humphreys (1989) theory of attentional engagement that states selection is most efficient when target-distractor similarity (TD similarity) is low or when distractor-distractor similarity (DD similarity) is high. When DD similarity is high the weight attached to each distractor becomes linked meaning that when one distractor is suppressed, all are suppressed (in their terminology: denied entry to visual short-term memory), facilitating target selection. Importantly, TD/DD similarity need not be restricted to a single dimension (e.g. the similarity in colour between/within target/distractors). For instance, search items may be 'similar' in accordance with the Gestalt principles of proximity (e.g. Mack, Tang, Tuma, Kahn, & Rock, 1992), common fate (e.g. Duncan, 1995; Levinthal & Franconeri, 2011), closure (e.g. Kramer & Jacobson, 1991), and continuity (i.e. collinearity; e.g. Jingling, Tang & Tseng, 2013; Jingling & Tseng, 2013; Jingling & Zhaoping, 2008). In Chapter 6 the IF paradigm will be used to investigate the effects of size similarity and proximity grouping on target selection. Because of the unpredictable nature of both the IF presence/coincidence and the target colour top-down control should be minimal (as shown by the results of Chapter 5). This allows bottom-up grouping effects promoted by the irrelevant size dimension to be examined.

The displays used in the present experiments are illustrated in Fig. 6.1. In Fig. 6.1C the size IF coincides with both of the distractors (tDD). Hence, the distractors are also closer together (n.b. in the present experiments a large item is created by increasing the size of the small item in all directions from the centre), promoting grouping by proximity. As a result the distractors should be more easily suppressed and search performance should be better than

baseline performance in the tdd condition. However, the displays may also be grouped according to size similarity. Thus, performance in the Dd display types might be reduced compared to DD and dd (depending on the relative weight attached to similarity and proximity grouping mechanisms). Furthermore, proximity and similarity grouping may demonstrate interactive effects. In this case Dd performance might be more disrupted when the target is large than when the target is small. In the TDd condition the distractors cannot be grouped by similarity, and at the same time the target is grouped by proximity with the large distractor. Thus performance may be worse here than in the tDd condition where, although the distractors cannot be grouped by similarity, the target is not grouped by proximity to the large distractor.

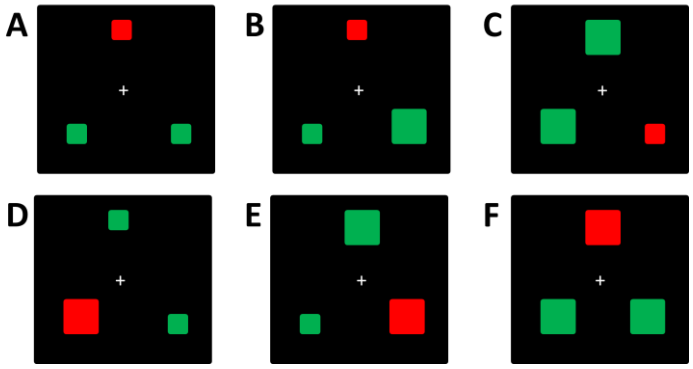

Fig. 6.1. Schematic representation of the factorial combination of display types used in Experiment 6.1 and Experiment 6.2.1. For simplicity the red square is the target and green squares are distractors in A-F although colour was unpredictable in all experiments in this chapter. A=All small (tdd), B=Small target, 1 large distractor, 1 small distractor (tDd), C=Small target, 2 large distractors (tDD), D=Large target, 2 small distractors (Tdd), E=Large target, 1 small distractor, 1 large distractor (TDd), F=All large (TDD).

6.0.3 The present studies

The presence of an IF has been shown to disrupt search performance (e.g. Theeuwes, 1992). This chapter investigated whether an IF coinciding with multiple items leads to grouping according to size similarity and/or proximity. Because of the novelty of the experimental design, Experiment 6.1 will investigate the effects of the IF coinciding with multiple items using a classic compound search paradigm relying on key-press responses. Subsequently the CRT methodology will be applied to investigate the time course of proximity and similarity grouping (see 6.2.1.1).

Experiment 6.1: Key-press Response Task

6.1.1 Introduction

It is unclear how an IF that is free to coincide with multiple search items influences target selection. In this first experiment participants were presented with a factorial combination of IF conditions (Fig. 6.1). The presence of the IF may promote proximity or size similarity grouping. In comparison to baseline performance (i.e. tdd) proximity grouping would be largely beneficial to search, whereas grouping by similarity would be largely disruptive. Moreover, performance may be particularly disrupted when similarity grouping is unable to group the distractors and the target is grouped by proximity to a distractor (i.e. the TDd display type). The first experiment investigates the grouping effects that emerge when a key-press is required to discriminate the target item. This provides an easily replicable design for future studies and offers a starting point for interpretation of the CRT results presented in Experiment 6.2.1.

6.1.2 Method

The method matched that of Experiment 5.1 with the following exceptions.

Participants. 17 University of Birmingham students (9 female, aged 18-22 (mean 18.8)) took part in the experiment in exchange for cash or course credit.

Stimuli. All trials were 3-item odd-colour search trials. On trials with an IF present one or more of the squares were larger than the other one/two (5.7° x 5.7° versus 3.8° x 3.8°). Because of the variable size of the items the methodology could not utilise Maljkovic & Nakayama's (1994) compound search paradigm presented in Experiment 3.3. This is because the size of the cut-off segment would be confounded by the size of the target producing faster RTs to the large target based on the response-defining feature. Instead, all 3 items were whole diamonds with either a black X or O (1° x 1°) presented centrally within each search item.

Design. Participants were required to identify the letter embedded within the odd-colour diamond, responding by pressing 'H' on a keyboard if an X was embedded and 'B' if an O was embedded. Participants completed 8 blocks of 96 trials with each block split into the six display types presented in Fig. 6.1. All combinations of target and distractor sizes were presented to the participant in a pseudorandom factorial design: (1) all small (tdd), (2) small target, 1 large distractor, 1 small distractor (tDd), (3) small target, 2 large distractors (tDD), (4) large target, 2 small distractors (Tdd), (5) large target, 1 small distractor, 1 large distractor (TdD), and (6) all large (TDD). For each display type the target and distractors appeared at each of the three possible positions. Target colour was also unpredictable, pseudorandomly selected on each trial to ensure a 50-50 split of red and green targets.

Dependent variables were RT and accuracy of letter identification. These measures were subject to a two-way ANOVA with factors target size (large vs. small) and distractor sizes (dd vs. Dd vs. DD).

6.1.3 Results

Results were collapsed across target colour, position and letter before outliers (RTs > 2 standard deviations from the mean per participant; 2.2%) were removed.

There were no main effects of target size ($F(1,16)=0.88$, $p>0.250$, $\eta_p^2=0.09$) or distractor sizes ($F(2,32)=0.34$, $p>0.250$, $\eta_p^2=0.04$) on letter identification accuracy, and no interaction ($F(2,32)=0.96$, $p>0.250$, $\eta_p^2=0.06$). Error trials were removed from further analysis (3.4% of trials).

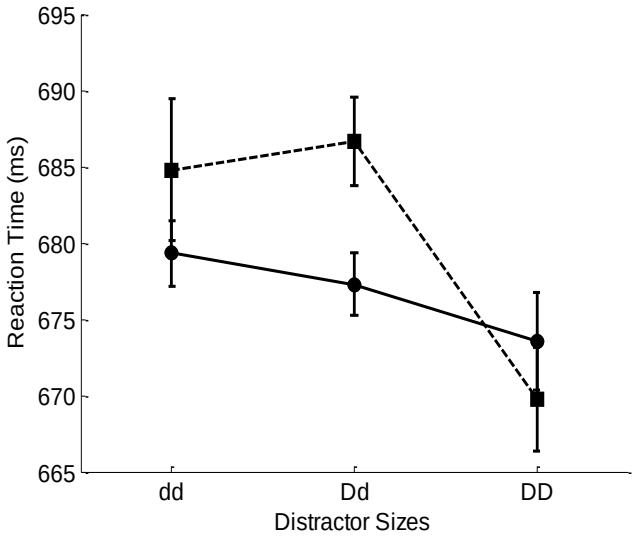

Fig. 6.2. The effects of target size (small = solid line, large = dashed line) and distractor sizes on key-press RTs. Error-bars represent within-subjects standard error (Cousineau, 2005).

The effects of target size and distractor sizes on RTs are illustrated in Fig. 6.2. There was no main effect of target size ($F(1,16)=2.20$, $p=0.16$, $\eta_p^2=0.12$) but a significant effect of distractor sizes on RTs ($F(2,32)=5.77$, $p=0.007$, $\eta_p^2=0.27$). Despite the target size x distractor sizes interaction not reaching significance ($F(2,32)=2.01$, $p=0.15$, $\eta_p^2=0.11$), the RT patterns are clearly different for large and small targets. Small targets show a trend for a linear

reduction in RTs from dd to DD ($t(16)=1.58$, $p=0.13$). Large targets also show a reduction from dd to DD ($t(16)=2.14$, $p=0.049$) but performance is worst at Dd. Indeed there is a significant difference between large and small targets at Dd ($t(16)=2.36$, $p=0.032$).

6.1.4 Discussion

The results showed that RTs tended to decrease as the size of the distractors increased. This is consistent with proximity grouping of the distractors facilitating target selection. However, the linear pattern of reduction according to distractor sizes was not present for the large target. RTs did decrease from dd to DD, as predicted by proximity grouping, but RTs increased when the distractors could not be grouped by similarity (Dd). This is explained by an interactive effect of proximity and similarity grouping that is influenced by the size of the target as well as the distractors. With the TDd display type the large target is grouped by proximity with the large distractor whilst the two distractors cannot be grouped by size similarity. Hence, it is doubly difficult to select the target item. On the one hand the unequally sized distractors cannot be linked and suppressed, and on the other hand the target appears close to the large distractor allowing it to be grouped by proximity. The combination of these processes has a disruptive influence on search. By comparison, with the tDd display type although the distractors cannot be grouped by similarity search is not disrupted because the target is not grouped by proximity with a distractor.

Interestingly, RTs were increased when participants were presented with a large target and two small distractors (Tdd). Under these conditions the literature on redundancy gains would predict the best performance (e.g. Zehetleitner, Krummenacher, & Müller, 2009). This highlights the importance of distractor proximity grouping – when such grouping is absent search suffers, even when the target is salient along two dimensions. Furthermore, the

redundancy effect for the Tdd condition may have been diluted regardless of the distractor sizes because the size of the target was not relevant for task completion (see Grubert, Krummenacher, & Eimer, 2011).

In summary, we have shown that an IF coinciding with more than one search item is able to facilitate search (e.g. tDD and TDD conditions) but with negative consequences when proximity and similarity grouping (i.e. TDd) are unable to segregate the target and distractors.

Experiment 6.2.1: Choice Reaching Task

6.2.1.1 Introduction

First and foremost, Experiment 6.2.1 set out to replicate the novel results of Experiment 6.1. We also aimed to investigate the time course of proximity and similarity grouping using the CRT.

Research has shown that proximity grouping and similarity grouping rely on distinct processes with grouping by proximity occurring faster than grouping by similarity (e.g. Ben-Av & Sagi, 1995; Han & Humphreys, 1999; Han, Humphreys, & Chen, 1999). For instance, Han et al. (1999) measured the time taken to discriminate global-level letters (H or E) comprised of local circles. Results showed that when the local circles could be grouped by proximity, discrimination times were faster than when grouped by similarity. Furthermore, investigations using ERP recordings have shown that proximity grouping modulates both early activity in medial occipital regions and late activity in occipito-parietal cortex, whereas similarity grouping by colour (Han, Ding, & Song, 2002) or shape (Han, Song, Ding, Yund, & Woods, 2001) modulates only late occipito-temporal activity (see also Han, 2004). In relation to the present study, we have already seen that temporally distinct processes can be

revealed in the IL and MD of the reach movement (Chapter 4). If proximity and similarity grouping influence target localisation at different time points we may be able to map these grouping processes onto the two reach parameters. To this end Experiment 6.2.1 applied the CRT methodology to the factorial IF design presented in Experiment 6.1.

6.2.1.2 Method

The method matched that of Experiment 6.1 with the following exceptions.

Participants. 17 University of Birmingham students (11 female, aged 18-21 (mean 19.1)) took part in the experiment.

Stimuli. All trials were 3-item odd-colour search trials. There was no letter presented within the search items. Instead participants reached and touched the odd-colour target.

Design. The same display types were used as in Experiment 6.1 (Fig. 6.1). Again, a two-way ANOVA with the within-subjects factors target size (large vs. small) and distractor sizes (dd vs. Dd vs. DD) was conducted with IL and MD as dependent variables. Significant main effects were investigated using paired-samples t-tests.

6.2.1.3 Results

Results were collapsed across target colour and position (both equally split across conditions) and error trials and outliers (2.8%) were removed. Error trials included incorrect target selections (<0.1%), and motion capture recording errors (<1%).

There was no main effect of target size on IL ($F(1,16)=1.01$, $p>0.250$, $\eta_p^2=0.06$) but there was a significant effect of distractor sizes ($F(2,32)=4.03$, $p=0.027$, $\eta_p^2=0.20$). There was no target size x distractor sizes interaction ($F(2,32)=0.63$, $p>0.250$, $\eta_p^2=0.04$). The pattern of results in Fig. 6.3A shows that the larger the distractors, the shorter the IL, supported by

longer ILs in dd than DD trials (t(16)=2.45, p=0.026). Despite the linear trend, differences between dd and Dd (p=0.21), and DD and Dd (p=0.11) did not reach significance.

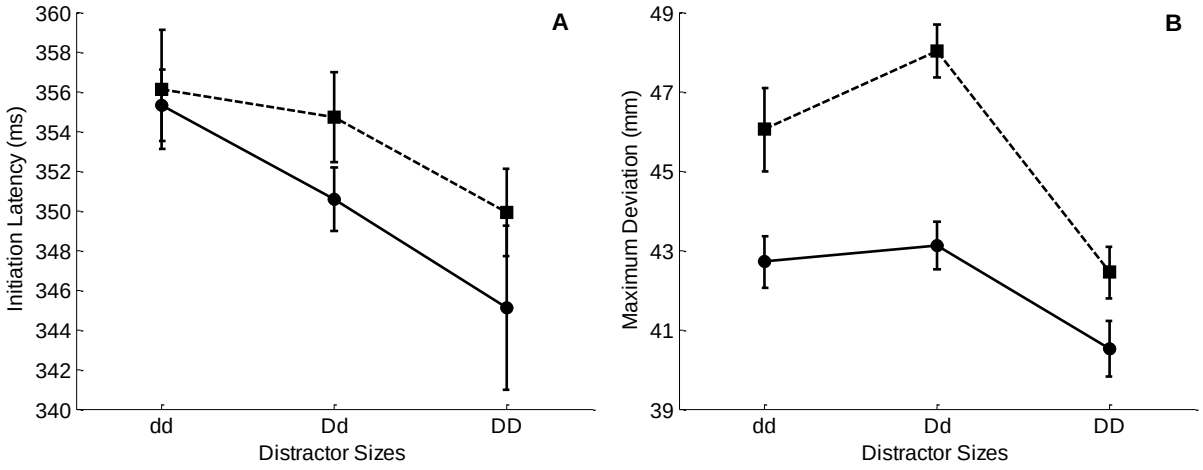

Fig 6.3. Effects of target size (small = solid line, large = dashed line) and distractor sizes on initiation latency (A) and maximum deviation (B) in Experiment 6.2.1. Error bars represent within-subjects standard error (Cousineau, 2005).

In terms of MD (Fig. 6.3B), there were main effects of both target size (F(1,16)=17.31, p=0.001, η_p^2=0.52) and distractor sizes (F(2,32)=17.43, p<0.001, η_p^2=0.52) but no interaction (F(2,32)=2.09, p=0.14, η_p^2=0.12). Large target reach trajectories showed greater deviation than reaches to small targets (46.14mm vs. 42.34mm). The effect of distractor sizes on MD was clearly different to the effect on IL. In MD the linear pattern is not observed. Although there was a significant decrease from dd to DD trials (t(16)=3.39, p=0.004), there was a marked increase from DD to Dd trials (t(16)=7.12, p<0.001) and a trend to an increase from dd to Dd trials (t(16)=1.77, p=0.097). Although the target size x distractor sizes interaction did not reach significance, Fig 6.3B shows that the disruptive effect of Dd was stronger for the large target (dashed line) than for the small target (solid line). To

illustrate this point the difference between dd and Dd is five times larger for the large target than the small target. This is analogous to the key-press results from Experiment 6.1 where the TDd condition showed most disruption.

6.2.1.4 Discussion

The results demonstrated a dissociation of grouping effects on IL and MD. IL reduced as the distractor sizes increased consistent with proximity grouping guiding early selection. MD also showed a reduction from DD to dd in line with proximity grouping but performance decreased when the distractors could not be grouped by similarity. That proximity grouping exerted early and ongoing influences on selection whereas similarity grouping effects were restricted to later processing is in accordance with ERP evidence (Han et al., 2002), and the tendency of proximity to exert stronger influences on selection than other perceptual features (Duncan & Humphreys, 1989).

Furthermore, the decrease in performance in the Dd condition was most marked with a large target: As with Experiment 6.1, performance was worst when the target was grouped by proximity with a distractor and the two distractors could not be grouped by similarity. However, the interaction between target size and distractor sizes did not reach significance. It is possible that the size of the target influenced the MD of the reach via motor rather than attentional processes. Thus, the main effect of target size may have obscured the attentional effects of grouping and masked any interaction. Experiment 6.1.2 will provide a baseline measure whereby participants reach and touch a single target. If reaches to large targets show greater MD than small targets this would account for the separation of the lines in Fig. 6.3B, and subsequently the lack of interaction that would reveal the combined effects of proximity and similarity grouping in the TDd condition.

Experiment 6.2.2: Single Target Control Task

6.2.2.1 Introduction

It may be that in Experiment 6.2.1 the reduction in performance in the TDd condition failed to reach significance because of motor-related influences of target size. To gain a better understanding of the results from Experiment 6.2.1 this experiment will ask participants to reach to a large or small target in the absence of any distractors. The effects of target size manipulations are described by Fitts's law (Fitts, 1954). This states that the time taken to reach a target is determined by its distance from the start location and its size (width): the closer and/or larger the target the faster the reach is completed. Whilst Fitts's law does not make reference to the time taken to initiate the movement or the deviation of the trajectory, it does offer an explanation for why large targets might show increased MD. In essence, the shorter movement duration may produce greater deviation resulting in a speed-accuracy trade off. As well as having shorter movement durations (and subsequently greater MD), the increased size may also afford a greater margin for error. In this case curved reach trajectories to the large target should be accompanied by more variable end-point accuracy. Thus, as well as examining IL and MD this experiment will also observe target size effects on movement duration and end-point variance.

6.2.2.2 Method

The method matched that of Experiment 6.2.1, with the following exceptions.

Participants. 9 University of Birmingham students (5 female, aged 18-23 (mean 19.4)) took part in this experiment in exchange for course credit.

Stimuli. All trials presented participants with either small (3.8° x 3.8°) or large (5.7° x 5.7°) single targets. The targets were positioned at the same locations as in previous experiments (i.e. 12 o'clock, 4 o'clock, or 8 o'clock).

Design & analysis. Participants completed 4 blocks of 96 trials with each block split equally into large and small target trials. Target colour was again unpredictable.

The following dependent variables were subject to paired-samples t-tests comparing large and small targets: IL, MD, movement duration, and end-point variance. As in Experiment 2.1, movement duration (ms) was calculated as the time at which the index finger velocity dropped below 20mm/s following movement initiation. End-point variance refers to the average variance (calculated separately in X (left-right) and Z (up-down) dimensions) of the position of first contact with the target item. This variance is computed per participant for large and small targets averaged across the three target positions.

6.2.2.3 Results

Results were collapsed across target colour and position (both equally split across conditions) and motion capture recording errors (<1%) and outliers (1.1%) were removed.

There was no difference in IL between large and small targets (Fig. 6.4A; $t(8)=0.35$, $p>0.250$, $d=0.14$), yet reaches to large targets exhibited significantly greater MD (Fig. 6.4B; $t(8)=3.61$, $p=0.007$, $d=1.22$). Both of these findings match those from Experiment 6.1.1. The question that remains is why do reach trajectories to large targets show greater deviation than small targets? The fact that large target reaches show shorter movement duration than small target reaches (Fig. 6.4C; $t(8)=2.68$, $p=0.028$, $d=0.91$) suggests that the greater deviation may be the result of a speed-accuracy trade off producing faster movements with increased curvature. This shorter movement duration and increased MD is possible due to the greater

margin for error with larger item size. This is supported by increased end-point variance in X (Fig. 6.5A; $t(8)=3.31$, $p=0.011$, $d=1.10$) and Z (Fig. 6.5B; $t(8)=2.58$, $p=0.032$, $d=0.86$) dimensions of reaches to large versus small targets.

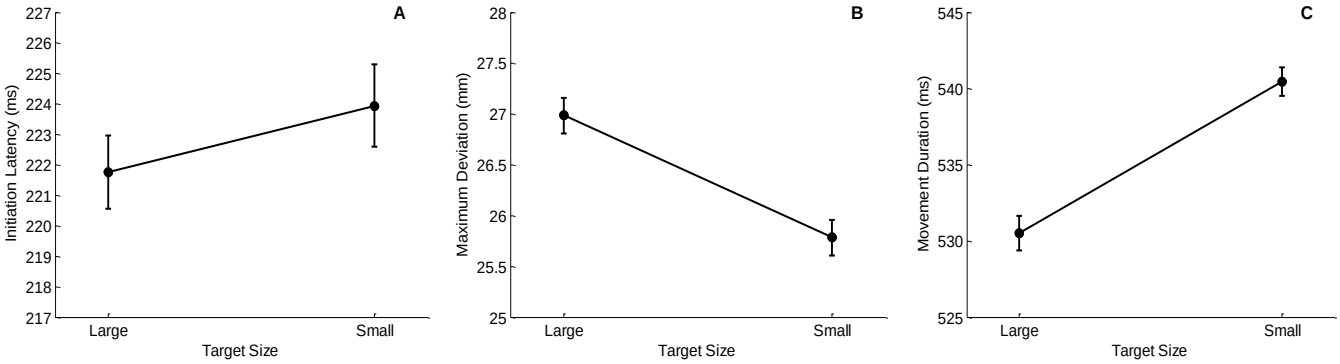

Fig 6.4. Effects of target size on initiation latency (A), maximum deviation (B), and movement duration (C) in Experiment 6.1.2. Error bars reflect within-subjects standard error (Cousineau, 2005).

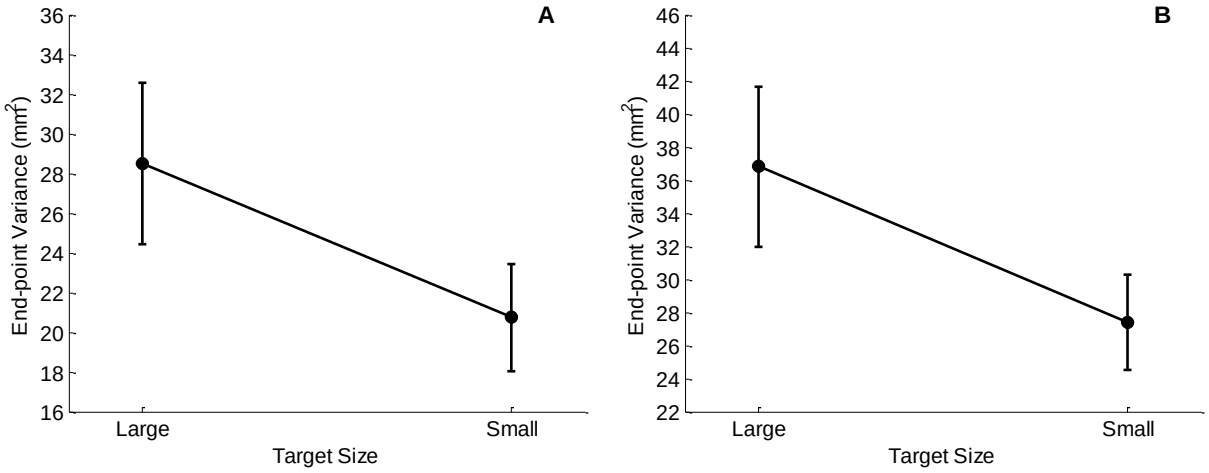

Fig. 6.5. End-point variance of reach movements to large and small targets in X (A) and Z (B) dimensions during Experiment 6.2.2.

6.2.2.4 Discussion

In the absence of distractor competition the results of Experiment 6.2.2 showed that the size of the target had no effect on IL but large targets showed increased MD, in line with predictions from Fitts's law (1954). This also replicates the target size main effects from Experiment 6.2.1. This suggests that the increase in MD for large versus small targets is motor-related. If we were to remove this motor effect (i.e. align the solid and dashed lines of Fig. 6.3B at baseline performance in the dd conditions) the results would closely resemble the key-press results of Experiment 6.1. Here, the effects of proximity and similarity grouping would emerge facilitating performance except in the TDd condition.

6.3 General discussion

The aim of the present chapter was to examine whether an IF coinciding with multiple search items was able to facilitate target selection via perceptual grouping. The results of Experiment 6.1 showed that key-press response times were faster when the large items promoted proximity grouping. However, when the target was grouped by proximity with a distractor and the two distractors could not be grouped by similarity (TDd) response times were increased. Thus, when the IF could coincide with multiple items search performance was modulated by resultant proximity and similarity grouping effects.

Experiment 6.2.1 applied the same IF design to the CRT. There were two main goals. Firstly, we wanted to replicate the novel results of Experiment 6.1. Secondly, by using the CRT we examined whether proximity and similarity grouping could be dissociated using IL and MD in a similar manner to early and late scene processing in Chapter 4. ILs were reduced in accordance with proximity grouping. MD also reduced from dd to DD but with an increase at Dd. This suggests that similarity grouping was influencing later target selection processes. The increase at Dd was particularly apparent with the large target, although the target size x

distractor sizes interaction failed to reach significance. Experiment 6.2.2 investigated why this might have been the case. Reaches to single large targets exhibited greater MD than reaches to single small targets. Thus, motor-related influences, such as the greater margin for error afforded by the large target, may have obscured the interaction between target size and distractors sizes in Experiment 6.2.1. If the difference in MD at baseline (dd) between large and small targets was reduced based on the results of the single target reaches, then the MD results would closely resemble the key-press findings of Experiment 6.1.

The fact that IL was influenced by proximity grouping and MD by a combination of proximity and similarity grouping is consistent with ERP recordings showing early and late effects of proximity grouping, and an exclusively late effect of similarity grouping (Han et al., 2001, 2002). Again, this highlights the ability of the CRT to separate temporally distinct influences on behaviour.

Moreover, the results of the present experiments highlight the complementary nature of CRT and key-press methodologies. Without the initial key-press study it would have been difficult to interpret the IL and MD results of Experiment 6.2.1. Using only one of the methodologies would likely have limited our understanding of either the nature or the time course of the IF-driven grouping influences. That both are able to demonstrate IF interference effects adds more support to the notion of a single effector-unspecific saliency map underlying target selection (see Zehetleitner, Hegenloh, and Müller (2011), for evidence for key-press responses and reaching movements).

The idea that an IF coinciding with multiple search items can guide search is an important step forward in our understanding of target selection. However the generalisability of the current findings warrants further investigation. For instance, search was facilitated by proximity grouping when the size IF coincided with two distractors. This grouping may not

have had such an impact if distractor numbers were increased since the two large distractors may have been segmented from the remaining small distractors as well as from the target item. This would result in multiple homogenous groups of search items (e.g. a group of small green distractors and a group of large green distractors surrounding a red target). Indeed, under these circumstances the reduction in distractor-distractor similarity should disrupt search (Duncan and Humphreys, 1989). More generally, it may be that IFs are used to guide search only when the task is relatively difficult, such as when two distractors compared to five or eleven distractors surround the target (Song & Nakayama, 2006). Future research may wish to address these issues to determine the scope of IF facilitation. Nevertheless, the studies presented in Chapter 6 provide an intriguing starting point for such investigations.

CHAPTER 7

General Discussion

7.1 Introduction

This body of work aimed to demonstrate how hand movements reveal the temporal characteristics of visual attention. To this end, we applied the choice reaching task (CRT) to a variety of visual search experiments. Consistent with the notion that cognitive processes can 'leak' into the reaching movement, we were able to examine perceptual priming effects (Chapters 2, 3 and 4), global-to-local scene processing (Chapter 4), and irrelevant feature (IF) interference/facilitation (Chapters 5 and 6). Importantly, the results went beyond simple replications of key-press results, enabling insight into the time course of cognitive processes surpassing that which can be gained by RT measures alone.

7.2 Summary of thesis

The first experimental chapter conducted a closer examination of the CRT investigating whether peak velocity variables were able to advance our understanding of target selection. The peak velocity and time of peak velocity measures failed to provide additional insight beyond that gained from timing variables (particularly initiation latency; IL) and the maximum deviation (MD) of the reach trajectory. When the number of velocity peaks was entered as an independent variable it influenced reach parameters in a similar manner to a curved versus straight trajectory distinction. The only difference was that there was an overall time cost for trials with multiple velocity peaks whereas the shorter IL for curved trials overcame the longer movement duration (as in Song & Nakayama, 2008). This suggests that trials with more than one velocity peak are those trials where the selection process goes most awry. Hence, the discrete nature of the velocity peaks measure meant it was insensitive to less pronounced selection errors. For the remaining chapters the IL and MD variables were used as indices of selection. It was clear that MD was increasing when distracting items were present

but it was less clear where the reach deviated towards. We showed that most reaches were directed towards the target item or intermediate between the target and a distractor. This indicates that selection was either completed successfully or was still ongoing at movement onset with the reach directed towards the region of highest activation rather than a particular stimulus location. Curved reaches were often directed towards a distractor suggesting the distractor had reached the selection threshold prior to movement onset. These results are consistent with the dynamic competition between search items that forms the theoretical basis of the CRT. As further validation of our CRT paradigm we then replicated the results of Song and Nakayama (2006) showing colour priming of pop-out (PoP) biases on IL and MD.

The next two chapters also utilised priming paradigms. In Chapter 3 we used the probabilistic repetition of target colour to probe the involvement of the motor system in selecting/localising predictable targets. Based on previous research (e.g. Bestmann, Harrison, Blankenburg, Mars, Haggard et al., 2008) we expected tDCS over the motor system to modulate performance when the target colour was highly predictable (Experiment 3.2) but not when it was unpredictable (Experiment 3.1). This was shown to be the case with a stronger priming effect in the anodal stimulation condition compared to sham and cathodal conditions. This modulation was specific to MD rather than IL, and to reach responses rather than key-press RTs (Experiment 3.3). The lack of IL effect could be explained by the warning tone that may have normalised ILs across sessions and stimulation groups but is also consistent with prior work showing tDCS effects on online control but not onset latencies (e.g. Galea, Vazquez, Pasricha, Orban de Xivry, & Celnik, 2011; Hunter, Sacco, Nitsche, & Turner, 2009). The lack of RT effect indicates that the predictable target must be an endpoint of an overt movement for the recruitment of the motor system, unless the predictability is explicitly cued (e.g. Bestmann et al., 2008).

Rather than colour priming Chapter 4 used position and configural priming to test whether reaching movements are affected by the global-to-local cascade of scene processing. We demonstrated a dissociation of IL and MD that is consistent with global-to-local processing: ILs were influenced by configural priming (global-level) whilst MD was modulated by position priming (local-level). The distribution of initial reach angles suggests that this dissociation is not simply due to the participant initiating their reach to any search item before correcting the movement once the target has been selected. Furthermore, the effects on IL were immune to changes in configural priming probability whereas MD was increased when target repeats were less likely. This indicates a susceptibility of local-level processing to top-down biases and the reliance of rapid, global-level processing on bottom-up computation. Experiment 4.4 added an extra element to the search array creating square/diamond configurations. Consequently configural priming effects were reduced – performance was still worst when the configuration switched but previous distractor ILs were longer than previous target ILs. This suggested that position priming biases had begun to be reflected in the early movement phase and that adding the extra search item had expedited the progression of processing from global-to-local levels.

The final two chapters were both concerned with the impact of irrelevant features (IFs) on search performance. Chapter 5 investigated how two top-down factors, the search mode employed by the participant (cf. Bacon & Egeth, 1994) and the predictability of the IF presence (cf. Müller, Heller, & Ziegler 1995; Müller, Reimann, & Krummenacher, 2003), modulated the influence of the IF. When the target colour remained constant, allowing feature search mode to be deployed, the IF failed to capture attention even when its presence was unpredictable (Experiment 5.1). This argued against Theeuwes (1992) notion of compulsory attentional capture by a salient distractor IF and was also inconsistent with previous work

showing capture by an unpredictable IF in feature search mode (e.g. Geyer, Müller, & Krummenacher, 2008). Conversely, when the target colour was unpredictable, forcing participants to deploy singleton detection mode, the IF did capture attention but only when its presence was unpredictable (Experiments 5.2.1 and 5.2.2). This suggests a hierarchy of top-down control over IF interference. Firstly, if feature search mode is engaged no attentional capture occurs regardless of IF predictability. If feature search mode is not possible then singleton detection mode is engaged. If the presence of the IF is predictable then weight is shifted towards the target-defining dimension meaning the IF still does not capture attention. Capture only occurs in singleton detection mode with an unpredictable IF. The resulting interference was observed on early and late indices of attention (Experiment 5.2.2).

Finally, Chapter 6 examined whether the coincidence of an IF with more than one search item promoted bottom-up grouping. This was shown to be the case: Performance improved when the IF coincided with two distractors as this promoted grouping by proximity. Performance was reduced when the size IF promoted grouping by similarity. This detrimental effect on performance was particularly evident when the distractors were different sizes and the target was grouped by proximity to a distractor (TDd). Furthermore, in the CRT (Experiment 6.2.1) proximity grouping influenced both IL and MD whilst similarity grouping effects were restricted to MD. This is in line with ERP findings showing early and ongoing modulation of activity by proximity grouping but only late modulation by similarity grouping (Han, Ding, & Song, 2002).

7.3 The joys of choice reaching

Many of the visual search phenomena investigated in this thesis have been previously examined using key-press response tasks. The primary reason for using the CRT is that it

allows insight into the selection process as it unfolds over time (see Song & Nakayama, 2009; for a review). This was particularly evident in the results of Chapter 4. For the first time we were able to use the CRT to index global-level processing mapping configural priming effects onto IL, as well as local-level position priming effects on MD. Indeed, to the author's knowledge, this is the first time that a behavioural technique has been able to demonstrate the cascade of scene processing from global-to-local levels without changing the task demands (see 4.5). If we had relied on RTs to test our prediction that configural precedes position priming, the early influence of configuration would have been overlooked, as shown by Experiment 4.1.2. Only by using the CRT did we demonstrate the progression of processing from global- to local-levels.

Furthermore, the temporal separation of IL and MD means that the CRT is also able to infer bottom-up and top-down influences on selection. This is based on the logic that goal-directed top-down processes take longer to deploy than stimulus-driven bottom-up processes (e.g. Hein, Rolke, & Ulrich, 2006; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989), hence IL should index bottom-up and MD should index top-down effects. Note that this is not to say that top-down effects cannot occur even before the onset of the movement (e.g. baseline shifts in activity; e.g. Chapter 5; Chawla, Rees, & Friston, 1999; Zhang & Luck, 2009) but that in the absence of baseline shifts bottom-up biases usually precede top-down modulation. This allowed us to reveal the top-down impact of priming probabilities on local-level but not global-level processing in Chapter 4 (cf. Geyer & Müller, 2009), and the sustained influence of bottom-up attentional capture on early and late selection when no top-down control was available in Chapter 5 (Experiment 5.2.2).

However, the CRT methodology does not render RT measures redundant. Indeed, when used in combination the CRT and key-press paradigms may offer greater insight into

attentional processing. This was highlighted in Chapter 6. Here, the CRT measures were somewhat confounded by the changing size of the target (as shown in Experiment 6.2.2). As a result the interaction between similarity and proximity grouping on MD was obscured (Experiment 6.1). Without combining the key-press and CRT methodologies it is unlikely that we would have been able to paint as complete a picture of proximity and similarity grouping effects caused by an IF coinciding with multiple search items.

7.3.1 Initiation latency & maximum deviation

It is worth discussing what it is that the two main outcome measures, initiation latency and maximum deviation, are actually reflecting beyond "early and late selection processes". Recall that in Experiment 4.4 the pattern of configural priming effects on IL was slightly different to those reported in the three-item experiments. It was hypothesised that the faster progression from global to local levels resulted in position priming effects influencing IL where previously they were restricted to MD. Of course, throughout this thesis we have demonstrated that IL is sensitive to subtle biases on selection with faster ILs when the target colour repeats, when the target appears within a repeated configuration, when distractors are grouped by proximity etc. However, the IL captures these effects because the underlying processing happens to unfold around the time at which the reach is initiated. In Experiment 4.4 the processing of the configuration was seemingly completed before it was possible to initiate the reach. This meant that IL was unable to reflect configural processing. The reach trajectory provides insight into how successful the initial selection decision was and the biases that influence how efficiently the target can be re-selected following an erroneous decision. Again, such biases need to play out within a certain time window in order to influence the MD measure: if they occur too early competition between search items can be resolved prior to initiation producing a straight reach trajectory. Thus, the CRT is particularly well suited to

tasks that require relatively difficult selection decisions that cannot be resolved prior to initiation. Such tasks may range from three-item search tasks like those typically employed in this thesis to higher-order decision making (McKinstry, Dale, & Spivey, 2008) and lexical processing (Spivey, Grosjean, & Knoblich, 2005).

Another important issue is the combination of attentional and motor processes underlying the CRT. Throughout the thesis these two facets have been stated to work in parallel, in accordance with Song and Nakayama's (2009) 'leakage' hypothesis. This means that there is concurrent accumulation of sensory evidence (i.e. attentional competition) and programming of motor plans for each potential target location. The dorsal premotor area has been shown to carry out this accumulation of evidence and parallel generation of movement plans to distinct targets (Cisek & Kalaska, 2005). Theoretically, the selection decision and the effects on IL and MD can be described by diffusion models of attention (e.g. Palmer, Huk, & Shadlen, 2005; Smith & Ratcliff, 2004). When one of the stimulus locations reaches a decision bound the corresponding motor plan is selected and executed. Thus, IL reflects the point at which this initial decision bound is reached. Perceptual evidence then continues to accumulate (see Resulaj, Kiani, Wolpert, & Shadlen, 2009). If the selection of the target is confirmed then the reach trajectory continues towards where it was originally aimed and MD is low. However, if the evidence suggests an incorrect initial decision a change of mind bound is achieved and a different motor plan is affected. By using a double-step paradigm, where the target jumps post-initiation, Song and Nakayama (2008) showed that the time taken to re-select a different motor plan based on incoming evidence is approximately 150ms. Because this approximates the time of MD in the CRT it suggests that MD is reflecting the point shortly after the change of mind bound is reached when it is possible to select the corresponding motor plan.

7.4 Theoretical implications

Throughout the thesis the CRT was used to investigate a wide range of topics both within the sphere of attentional processing (e.g. PoP, global-to-local scene processing, IF modulation) and beyond (e.g. the role of the motor system in generating predictions). The following section attempts to synthesise the findings into a broad theoretical framework.

7.4.1 Target selection over time

The clearest contribution of the current work concerns the time at which different attentional processes and biases occur. Our findings suggest that, prior to and following the presentation of a busy visual scene, the processing that takes place can be split into three epochs (see Fig. 7.1). The procession of processing through these time points draws on established theoretical models, particularly Guided Search (Wolfe, 1989, 2007) and Reverse Hierarchies Theory (RHT; Hochstein & Ahissar, 2002).

First, prior knowledge of the target identity can cause baseline shifts in neural activity toward the target-defining feature (e.g. Zhang & Luck, 2009) facilitating the subsequent response (e.g. Chapter 5; Melcher, Papathomas, & Vidnyanszky, 2005). In the latest formulation of Guided Search (GS4; Wolfe, 2007) each relevant search dimension is represented by a number of distinct 'channels'. For instance, the colour dimension comprises channels for red, green, blue etc. When the target identity is known beforehand the weight attached to the output of the channel representing that feature (e.g. red) is increased. According to GS4, the weighting can also be changed based on trial-to-trial learning. The selection of one channel over another is based on the largest signal favouring the target versus the average signal for the distractors. The weight attached to this channel is carried forward on the next trial, and so on and so forth over consecutive activations until performance

reaches floor levels. The results of Experiment 2.2 suggest that the weighting of the target-defining channel reaches its floor level relatively quickly (i.e. within six colour repetitions). Furthermore, the results of Experiment 5.1 indicate that pre-onset modulation of the weight attached to the learned target colour is able to overcome attentional capture, even when the presence of the irrelevant feature is unpredictable.

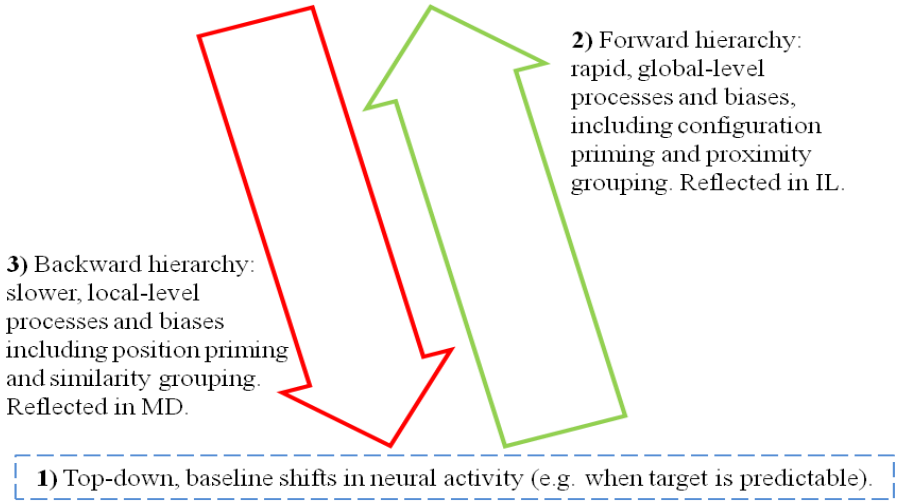

Fig. 7.1 Hypothesised time course of processing when presented with a visual scene. Firstly, if the target identity is predictable baseline shifts in activity help overcome target-distractor competition (e.g. Zhang & Luck, 2009). Secondly, in the absence of such attentional setting, processing proceeds through the forward hierarchy, reaching conscious awareness at the top of the hierarchy where high-level scene representations are manifested. Biases on such representations are indexed by IL. Finally, re-entry into previous lower-level processing occurs. Here local biases are revealed through MD. The figure is adapted and extended from Hochstein and Ahissar (2002).

In circumstances where baseline shifts in activity are not possible (e.g. when the target colour changes randomly from trial-to-trial) the selection process is susceptible to various biases described in the preceding chapters. The order in which many of these biases take

effect can be described using RHT. To recap, RHT states that stimulus processing only becomes available to conscious awareness when processing reaches higher levels. Lower-level features such as contrast, size, colour and orientation are still processed first but this processing is implicit. Only when processing reaches the top of the hierarchy can it be accessed and it is here that we perceive the overall 'gist' of the scene. So our earliest access to the attended object ("vision at a glance") reveals its abstract form. Biases on these representations, such as configural priming (Chapter 4) and proximity grouping (Chapter 6), are revealed by ILs that coincide with such processing. GS4 (Wolfe, 2007) also accounts for configural priming effects by including a secondary pathway that circumvents the bottleneck restricting selection (the same pathway is also used to rapidly extract average statistics from visual scenes; e.g. Ariely, 2001). Irrespective of the theoretical account, initial processing (revealed in reach ILs) is able to provide a representation of high-level scene properties that we have shown to be influenced by configural priming and proximity grouping.

Finally, if we want to more closely examine an aspect of an object ("vision with scrutiny") we must re-enter the processing pipeline. At this point biases on local-level processing occur that produce position priming effects (Chapter 4), similarity grouping effects (Chapter 6), and that can be disrupted by the presence of an irrelevant feature when attentional setting was unavailable (Chapter 5). RHT is consistent with the procession of visual input through the visual system (e.g. Juan, Campana, & Walsh, 2004). Low-level features are extracted in V1 and V2 before being processed by V3, V4 and area MT that begin to represent global features. Broader categorisation then occurs further upstream in inferotemporal and prefrontal regions (e.g. Afraz, Kiani & Esteky, 2006). The results of Chapter 2 suggest that even the motor cortex is involved in selection when the item represents the end point of an overt movement. Crucially, feedback loops from regions implicated in

later processing to lower-level areas offer the neural basis for the re-entry required for vision with scrutiny (e.g. Hock, Schöner, Brownlow, & Taler, 2011; Lamme, Super, & Spekreijse, 1998). To be clear, we view the feedforward side of the hierarchy in terms of anatomical complexity for perceptual processing: the further up the feedforward hierarchy, the more complex the perceptual representation and the more high-level the anatomical structure. Only on the feedback side of the hierarchy are we able to re-enter more basic perceptual processing carried out in lower anatomical areas.

The results of the studies in this thesis provide supporting evidence for both GS (Wolfe, 1989, 2007) and RHT (Hochstein & Ahsissar, 2002) and bring aspects of the two theories together to create a coherent framework. In addition, the findings presented also have theoretical implications within their particular field. These implications are discussed in the following sub-sections.

7.4.2 Dynamic competition. The first implication is for the theoretical basis of the CRT itself. The fact that initial incorrect and subsequent corrective movements are planned partly in parallel (Song & Nakayama, 2008; Experiment 2.2) provides evidence for the dynamic competition underlying the CRT. When a stimulus reaches the threshold for activation the reach is initiated towards that item. However, the results of Experiment 2.1 indicate that it is also possible that the activation threshold has not been achieved by any of the stimuli at the time of initiation. This is evidenced by the large number of reach trajectories that are initially directed to a region in between the target and distractor. Hence, the reach is seemingly directed towards the area of highest activation rather than a particular search item. In turn this indicates that an averaging process takes place whereby the activation of all search items is taken into account if the movement is initiated before any one item has reached the activation threshold. This is consistent with the manner in which dynamic competition is implemented in

a recent computational model of the CRT (Strauss & Heinke, 2012). It is also in close accordance with research showing that short-latency eye movements are initially directed in between search items/groups to the "centre of gravity" of activation (e.g. Findlay, 1982; He & Kowler, 1989). That reaching movements also reflect this averaging of activation is no surprise given the striking similarities displayed by reaching and eye movements when they are used to localise a target amongst distractors (e.g. McPeek, Maljkovic & Nakayama, 1999; McSorley, Haggard, & Walker, 2004; McSorley & Findlay, 2003; Song & McPeek, 2009; Zehetleitner, Hegenloh, & Müller, 2011).

7.4.3 The motor system. The results of Chapter 3 suggest that the motor system is involved in the guidance of target selection when the target feature is predictable. This corresponds with recent work implicating the motor system in cognitive processing previously thought to be completed 'upstream' (e.g. Bestmann, et al., 2008; de Lange, Rahnev, Donner, & Lau, 2013; Donner, Siegel, Fries, & Engel, 2009), and more specifically in the prediction of perceptual events (see Schubotz, 2007; for a review). However, the null effect of motor cortex tDCS on key-press responses (Experiment 3.3) argues against motor system involvement in general prediction. Instead, it suggests that the perceptual information must be movement-relevant (i.e. the end-point of an overt movement) for recruitment of the motor cortex. This is not to say that the motor cortex is not involved in general prediction when the upcoming target is explicitly cued (Bestmann et al., 2008) or that the premotor cortex is not involved in general prediction (Schubotz & von Cramon, 2002).

More broadly, that the trajectory of the reach is able to reflect ongoing attentional processing argues against the segmentation of the reach movement into pre-planned (i.e. feedforward) and online (i.e. feedback) components (e.g. Jeannerod, 1988; Woodworth, 1899). Rather, it is in support of recent theories that allow for constant updating of reach

movements depending on incoming sensory information (e.g. Saunders & Knill, 2003) and underlying dynamic competition between potential movement targets (e.g. Cisek & Kalaska, 2002, 2005; Resulaj, Kiani, Wolpert, & Shadlen, 2009).

7.4.4 Irrelevant features. For the first time, the results of Chapter 5 demonstrate how the search mode employed and the weight attached to the target dimension combine to suppress attentional capture by the IF. Only when both of these strategies fail to exert top-down control is the IF able to interfere with the selection process (Experiment 5.2.2). When the participant can employ feature search mode the IF fails to capture attention even during the early stages of selection (Experiment 5.1). This argues against Theeuwes (1992) theory of compulsory attentional capture and Theeuwes (2010) subsequent assertion that top-down control is restricted to later attentional processes. Furthermore, Chapter 5 presented novel evidence that the weight attached to the target/IF dimensions is taken into account when the participant deploys singleton detection mode. One of the main aims of the studies in Chapter 5 was to examine the time at which bottom-up and top-down capture occurred, hence the use of the CRT. Future studies may wish to replicate our results using a traditional key-press methodology (see 7.5 for future research).

The findings of Chapter 6 showed that IFs coinciding with multiple search items are able to facilitate search via grouping. Hence, the presence of an IF does not always lead to disruption. Moreover, the CRT provided behavioural evidence that grouping by proximity preceded grouping by similarity, adding to existing neurophysiological evidence (e.g. Han, Ding, & Song, 2002; Han, Song, Ding, Yund, & Woods, 2001).

7.5 Future research

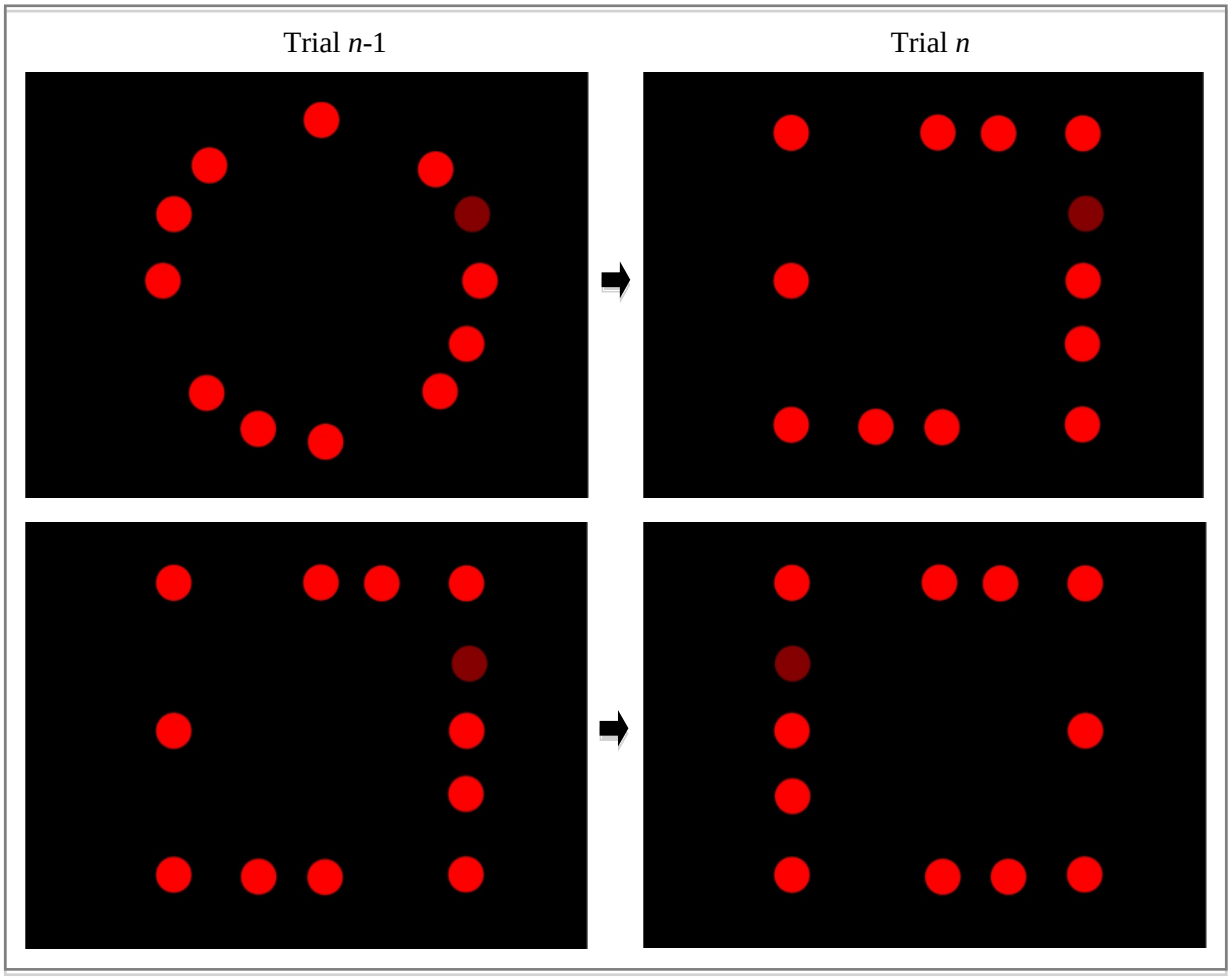

Fig. 7.2. Examples of the search displays used in new experiments within our laboratory. The top row illustrates a configuration switch but a previous target position priming condition from trial *n*-1 to trial *n*. The bottom row illustrates a configuration repeat but a previous empty position priming condition from trial *n-1* to trial *n*. A target-distractor contrast decision is required because the increase in distractors should enhance the target pop-out effect (e.g. Maljkovic & Nakayama, 1994). In turn this would make the task too simple with a red/green distinction.

With the exception of the colour PoP experiments (Chapter 2) this thesis presents novel applications of the CRT to different aspects of attentional processing. The exploratory nature

of the studies provides a starting point for future investigations that may wish to replicate and extend our principle findings. Indeed, work is already under way in our laboratory to further probe the progression from global- to local-level scene processing and overcome a limitation of the experimental design in Chapter 4. In these studies the configural priming and position priming conditions were highly correlated. When the configuration repeated the target could only appear at a previous target or distractor position, never at a previous empty location. Likewise, a configuration switch meant the target was always presented at a previous empty location. Our next set of experiments will use the displays presented in Fig. 7.2.

Using these displays removes the dependency of position priming conditions on configural priming, and vice versa. In the top row of Fig. 7.2 the target position is repeated but the configuration switches from a circle to a square. In the bottom row the target appears at a previous empty location despite the configuration repeating. This is made possible by overlapping certain positions within the configurations and changing others to form the circle or square outline. Because the number of distractors needs to be increased to form the 'overlapping' configurations presenting a green target amongst red distractors would increase the efficiency of the search task compared to the 3-item displays used in Experiments 4.2 and 4.3 (e.g. Maljkovic & Nakayama, 1994). As a consequence the IL of the reach may already begin to index position priming biases, as shown in Experiment 4.4. Therefore we will ask participants to select the odd-one-out based on a luminance comparison – i.e. "reach and touch the bright/dim red circle". We expect to replicate the results presented in Chapter 4, demonstrating configural and position priming biases on IL and MD, respectively. We will then extend our investigations examining, for example, whether increasing the probability of the target appearing in the top versus bottom half of the circle and the bottom versus top half of the square leads to greater configural priming biases (as the configuration may be weighted

more strongly when it provides specific information as to the likely target location). This would add to research showing faster target discrimination when a target is more likely to appear in one half of a display ('rich') versus the other ('sparse'; Jiang & Swallow, 2013; Jones & Kaschak, 2012; Druker & Anderson, 2010; Walthew & Gilchrist, 2006). Furthermore, such an effect would temper our conclusion that the configuration of the items is insensitive to top-down control. It may be the case that top-down position priming effects can also bias configural priming when the configuration offers valuable guidance to local-level processing. It would also be interesting to observe whether configural priming still exists when the physical location of the repeated configuration changes. For instance, the circular configuration may be presented in the top-right display quadrant on one trial and the bottom-left quadrant on the next trial. If configuration is encoded in object-centred (allocentric) coordinates facilitation should still exist. Conversely if the configuration is encoded in person-centred (egocentric) coordinates facilitation would be eradicated (see Ball, Smith, Ellison, Schenk, 2009; Neggers, van der Lubbe, Ramsey, & Postma, 2006).

Further research may also wish to extend the results of Chapter 5 by investigating the interaction between search mode and IF predictability using targets and IFs defined along other dimensions (e.g. an orientation-defined target in the presence of a luminance-defined IF). This would test the generalisability of the present findings which is particularly important given the added weight that seems to be attached to a target defined along the colour dimension (see Poisson & Wilkinson, 1992; Williams & Reingold, 2001; Zohary & Hochstein, 1989). Indeed, this suggests that IF interference may be greater when searching, for example, for an orientation-defined target rather than a colour-defined target that already receives attentional priority. Future studies using the CRT to examine IF interference may

benefit from using an IF defined by orientation, luminance, shape, etc., to overcome the effect of target size observed in the CRT results of Experiment 6.2.1.

Using IFs defined along different dimensions would also allow the examination of grouping according to different Gestalt laws. For instance, the presence of orientation IFs (e.g. vertically oriented bars in a colour-defined search task) may promote grouping by collinearity (cf. Jingling, Tang & Tseng, 2013; Jingling & Tseng, 2013; Jingling & Zhaoping, 2008). Depending on the temporal locus of collinearity grouping presenting bars that align vertically to create a 'ladder/snake' percept may disrupt early or late colour search.

7.6 Summary

This thesis used the CRT to shed light on attentional processing. It has shown how the CRT is able to index early and late influences on target selection, above and beyond those that can be observed using key-press responses. We presented the first applications of the CRT to a range of topics including, the involvement of the motor cortex in expectation-based guidance of target selection, the cascade of scene processing from global- to local-levels, and the disruptive and facilitatory influence of irrelevant features, as well as building on our understanding of the dynamic competition underlying the CRT. In some cases the CRT has replicated key-press response findings, for instance, by demonstrating focal attention effects of PoP on IL and MD. In other cases it has offered novel behavioural insight. For example, it has allowed us to observe (i) motor cortex involvement in the prediction of *movement-relevant* information; (ii) that global, configural processing precedes local, positional processing; (iii) that IFs interfere in early (bottom-up) and late (top-down) selection processes but only when the target identity and IF presence are unpredictable, and (iv) that grouping by proximity precedes grouping by similarity. Many of these findings represent the first

behavioural demonstration of such effects revealed in earlier neurophysiological studies. It is the author's view that future studies that combine the CRT with key-press response measures will provide greater insight into ongoing competition for attention than studies relying solely on discrete response times.

References

Adam, J. J., Parthoens, S., & Pratt, J. (2006). Distinct mechanisms for planning keypress and reaching responses: A developmental study. *Human Movement Science, 25,* 293-309.

Afraz, S. R., Kiani, R., & Esteky, H. (2006). Microstimulation of inferotemporal cortex influences face categorization. *Nature, 442,* 692-695.

Akyürek, E. G., & Schubö, A. (2011). The allocation of attention in displays with simultaneously presented singletons. *Biological Psychology, 87,* 218-225.

Anderson, B. A., Laurent, P. A., & Yantis, S. (2011). Value-driven attentional capture. *Proceedings of the National Academy of Sciences USA, 108,* 10367-10371.

Ansorge, U., Kiss, M., Worschech, F., & Eimer, M. (2011). The initial stage of visual selection is controlled by top-down task set: new ERP evidence. *Attention, Perception & Psychophysics, 73,* 113-122.

Ariely, D. (2001). Seeing sets: Representation by statistical properties. *Psychological Science, 12,* 157-162.

Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in Cognitive Sciences, 16,* 437-443.

Bacon, W. F., & Egeth, H. (1994). Overriding stimulus-driven attentional capture. *Perception & Psychophysics, 55,* 484-496.

Baker, S. C., Rogers, R. D., Owen, A. M., Frith, C. D., Dolan, R. J., Frackowiak, R. S., & Robbins, T. W. (1996). Neural systems engaged by planning: a PET study of the Tower of London task. *Neuropsychologia, 34,* 515-526.

Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Research, 50,* 999-1013.

Ball, K., Smith, D., Ellison, A., & Schenk, T. (2009) Both egocentric and allocentric cues support spatial priming in visual search. *Neuropsychologia, 47,* 1585-1591.

Belopolsky, A. V., Schreij, D., & Theeuwes, J. (2010). What is top-down about contingent capture? *Attention, Perception & Psychophysics, 72*, 326-341.

Ben-Av, M. B., & Sagi, D. (1995). Perceptual grouping by similarity and proximity: Experimental results can be predicted by intensity autocorrelations. *Vision Research, 35,* 853-866.

Bestmann, S., Harrison, L. M., Blankenburg, F., Mars, R. B., Haggard, P., Friston, K. J., & Rothwell, J. C. (2008). Influence of Uncertainty and Surprise on Human Corticospinal Excitability during Preparation for Action. *Current Biology, 18,* 775-780.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*, 433-436.

Bravo, M. J., & Nakayama, K. (1992). The role of attention in different visual-search tasks. *Perception & Psychophysics, 51,* 465-472.

Brown, L. E., Wilson, E. T., Goodale, M. A., & Gribble, P. L. (2007). Motor Force Field Learning Influences Visual Processing of Target Motion. *Journal of Neuroscience, 27,* 9975-9983.

Burra, N. & Kerzel, D. (2013). Attentional capture during visual search is attenuated by target predictability: Evidence from the N2pc, Pd, and topographic segmentation. *Psychophysiology, 50*, 422-430.

Caparos, S., Linnell, K. J., Bremner, A. J., de Fockert, J. W., & Davidoff, J. (2013). Does local/global perceptual bias tell us anything about local/global selective attention? *Psychological Science, 24*, 206-212.

Cave, K. R., & Wolfe, J. M. (1990). Modeling the role of parallel processing in visual search. *Cognitive Psychology, 22,* 225-271.

Chawla, D., Rees, G., & Friston, K. J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neuroscience, 2,* 671-676.

Cisek, P., & Kalaska, J. F. (2002). Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *Journal of Neurophysiology, 87,* 1149-1154.

Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron, 45,* 801-814.

Close, A., Sapir, A., Burnett, K., & d'Avossa, G. (2014). Attention to multiple location is limited by spatial working memory capacity. *Journal of Vision, 14(9)*: 17.

Conci, M., Müller, H. J., & Elliott, M. A. (2007). The contrasting impact of global and local object attributes on Kanizsa figure detection. *Perception & Psychophysics, 69,* 1278-1294.

Conci, M., Töllner, T., Leszczynski, M., & Müller, H. J. (2011). The time-course of global and local attentional guidance in Kanizsa-figure detection. *Neuropsychologia, 49,* 2456-2464.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3,* 201-215.

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorial in Quantitative Methods for Psychology, 1,* 42-45.

Dale, R., Kehoe, C. E., & Spivey, M. J. (2007). Graded motor responses in the time course of categorizing atypical exemplars. *Memory & Cognition, 35,* 15-28.

De Lange, F. P., Rahnev, D. A., Donner, T. H., & Lau, H. (2013). Prestimulus oscillatory activity over motor cortex reflects perceptual expectations. *Journal of Neuroscience, 33,* 1400-1410.

Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: Evidence for a common attentional mechanism in reaching and perception. *Visual Cognition, 5*, 81-107.

Desimone, R., & Duncan, J. (1995). Neural Mechanism of Selective Visual Attention. *Annual Review of Neuroscience, 18,* 193-222.

Dombrowe, I., Donk, M., & Olivers, C. N. L. (2011). The costs of switching attentional sets. *Attention, Perception, & Psychophysics, 73,* 2481-2488.

Donner, T. H., Siegel, M., Fries, P., & Engel, A. K. (2009). Buildup of Choice-Predictive Activity in Human Motor Cortex during Perceptual Decision Making. *Current Biology, 19,* 1581-1585.

Duncan, J. (1995). Target and nontarget grouping in visual search. *Perception & Psychophysics, 57,* 117-120.

Duncan, J., & Humphreys, G. W. (1989). Visual Search and Stimulus Similarity. *Psychological Review, 96,* 433-458.

Druker, M., & Anderson, B. (2010). Spatial Probability Aids Visual Stimulus Discrimination. *Frontiers in Human Neuroscience, 4,* 63.

Eckstein, M. P. (2011). Visual search: a retrospective. *Journal of Vision, 11(5)*: 14.

Egeth, H. E., Leonard, C. J., & Leber, A. B. (2010). Why salience is not enough: Reflections on top-down selection in vision. *Acta Psychologica*, 135, 130-132.

Egeth, H. E., & Yantis, S. (1997). Visual attention: Control, representation, and time course. *Annual Review of Psychology, 48*, 269-297.

Ehinger, K. A., Hidalgo-Sotelo, B., Torralba, A. & Oliva, A. (2009). Modelling Search for People in 900 Scenes: A combined source model of eye guidance. *Visual Cognition, 17,* 945-978.

Eimer, M. & Kiss, M. (2010). Top-down search strategies determine attentional capture in visual search: Behavioral and electrophysiological evidence. *Attention, Perception, & Psychophysics, 72,* 951-962.

Eimer, M., Kiss, M., Press, C., & Sauter, D. (2009). The roles of feature-specific task set and bottom-up salience in attentional capture: An ERP study. *Journal of Experimental Psychology: Human Perception and Performance, 35,* 1316-1328.

Eisenberg, M., Shmuelof, L., Vaadia, E., & Zohary, E. (2011). The Representation of Visual and Motor Aspects of Reaching Movements in the Human Motor Cortex. *Journal of Neuroscience 31,* 12377-12374.

Elliott, D., Hansen, S., Grierson, L. E. M., Lyons, J., Bennett, S. J., & Hayes, S. J. (2010). Goal-directed aiming: Two components but multiple processes. *Psychological Bulletin, 136,* 1023-1044.

Festman, Y., Adam, J. J., Pratt, J., & Fischer, M. H. (2013). Both hand position and movement direction modulate visual attention. *Frontiers in Psychology, 4*(657).

Findlay, J. M. (1982). Global visual processing for saccadic eye movements. *Vision Research, 22,* 1033-1045.

Fitts, P. M. (1954). The Information Capacity of the Human Motor System in Controlling the Amplitude of Movement. *Journal of Experimental Psychology, 47,* 381-391.

Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *Journal of Neuroscience, 5,* 1688-1703.

Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 1030-1044.

Galea, J.M., Vazquez, A., Pasricha, N., Orban de Xivry, J., & Celnik, P. (2011). Dissociating the roles of the cerebellum and motor cortex during adaptive learning: The motor cortex retains what the cerebellum learns. *Cerebral Cortex, 21,* 1761-1770.

Geyer, T., & Müller, H. J. (2009). Distinct, but top-down modulable color and positional priming mechanisms in visual pop-out search. *Psychological Research, 73,* 167-176.

Geyer, T., Müller, H. J., & Krummenacher, J. (2008). Expectancies modulate attentional capture by salient color singletons. *Vision Research, 48*, 1315-1326.

Geyer, T., Müller, H. J., & Krummenacher, J. (2007). Cross-trial priming of element positions in pop-out visual search is dependent on stimulus arrangement. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 788-797.

Geyer, T., Zehetleitner, M., & Müller, H. J. (2010). Positional priming of pop-out: a relational encoding account. *Journal of Vision, 10(2)*: 3.

Goffaux, V., Peters, J., Haubrechts, J., Schiltz, C., Jansma, B., & Goebel, R. (2011). From coarse to fine? Spatial and temporal dynamics of cortical face processing. *Cerebral Cortex, 21,* 467-476.

Gokce, A., Müller, H. J., & Geyer, T. (2013). Positional priming of pop-out is nested in visuospatial context. *Journal of Vision, 13(3)*: 32.

Grice, G. R., Canham, L., & Boroughs, J. M. (1983). Forest before trees? It depends where you look. *Perception & Psychophysics. 33,* 121-128.

Grubert, A., Krummenacher, J., & Eimer, M. (2011). Redundancy gains in pop-out visual search are determined by top-down task set: Behavioral and electrophysiological evidence. *Journal of Vision, 11(14)*: 10.

Han, S. (2004). Interactions between proximity and similarity grouping: An ERP study. *Neuroscience Letters, 367*, 40-43.

Han, S., Ding, Y., & Song, Y. (2002). Neural mechanisms of perceptual grouping in humans as revealed by high density event related potentials. *Neuroscience Letters, 319*, 29-32.

Han, S., & Humphreys, G. W. (1999). Interactions between perceptual organization based on Gestalt laws and those based on hierarchical processing. *Perception & Psychophysics, 61,* 1287-1298.

Han, S., Humphreys, G. W., & Chen, L. (1999). Uniform connectedness and classical Gestalt principles of perceptual grouping. *Perception & Psychophysics, 61,* 661-674.

Han, S., Song, Y., Ding, Y., Yund, E. W., & Woods, D. L. (2001). Neural substrates for visual perceptual grouping in humans. *Psychophysiology, 38*, 926-935.

Hatsopoulos, N. G., & Suminski, A. J. (2011). Sensing with the motor cortex. *Neuron, 72*, 477-487.

Hayden, B. Y., & Gallant, J. L. (2005). Time course of attention reveals different mechanisms for spatial and feature-based attention in area V4. *Neuron, 47,* 637-643.

He, P., & Kowler, E. (1989). The role of location probability in the programming of saccades: implications for 'center-of-gravity' tendencies. *Vision Research, 29,* 1165-1181.

Hecht, H., Vogt, S., & Prinz, W. (2001). Motor learning enhances perceptual judgment: a case for action-perception transfer. *Psychological Research, 65,* 3-14.

Hegde, J. (2008). Time course of visual perception: Coarse-to-fine processing and beyond. *Progress in Neurobiology, 84,* 405-439.

Hein, E., Rolke, B., & Ulrich, R. (2006). Visual attention and temporal discrimination: Differential effects of automatic and voluntary cueing. *Visual Cognition, 13,* 29-50.

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience, 18,* 604-613.

Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron, 36,* 791-804.

Hock, H. S., Schöner, G., Brownlow S., & Taler, D. (2011). The temporal dynamics of global-to-local feedback in the formation of hierarchical motion patterns: Psychophysics and computational simulations. *Attention, Perception & Psychophysics, 73,* 1171-1194.

Hübner, R., & Volberg, G. (2005). The integration of object levels and their content: A theory of global/local processing and related hemispheric differences. *Journal of Experimental Psychology: Human Perception and Performance, 31,* 520-541.

Hummel, F. C., Heise, K., Celnik, P., Floel, A., Gerloff, C., & Cohen, L. G. (2010). Facilitating skilled right hand motor function in older subjects by anodal polarization over the left primary motor cortex. *Neurobiology of Aging, 31,* 2160-2168.

Humphreys, G. W. & Müller, H. J. (1993). Search via Recursive Rejection (SERR): A connectionist model of visual search. *Cognitive Psychology, 25,* 43-110.

Humphreys, G. W., Stalmann, B. J., & Olivers, C. (2004). An analysis of the time course of attention in preview search. *Perception & Psychophysics, 66,* 713-730.

Hunter, T., Sacco, P., Nitsche, M. A., & Turner, D. L. (2009). Modulation of internal model formation during force field-induced motor learning by anodal transcranial direct current stimulation of primary motor cortex. *Journal of Physiology, 587,* 2949-2961.

Itti, L., & Koch, C. (2001). Computational Modelling of Visual Attention, *Nature Reviews Neuroscience, 2,* 194-203.

Jeannerod, M. (1988). *The neural and behavioral organization of goal-directed movements*. Clarendon Press, Oxford.

Jiang, Y. V., & Swallow, K.M. (2013). Spatial reference frame of incidentally learned attention. *Cognition, 126,* 378-390.

Jingling, L., Tang, D. L., & Tseng, C-H. (2013). Salient collinear grouping diminishes local saliency in visual search: an eye movement study. *Journal of Vision, 13(12)*: 6.

Jingling, L., & Tseng, C-H. (2013). Collinearity impairs local element visual search. *Journal of Experimental Psychology: Human Perception and Performance, 39,* 156-167.

Jingling, L., & Zhaoping, L. (2008). Change detection is easier at texture border bars when they are parallel to the border: Evidence for V1 mechanisms of bottom-up salience. *Perception, 37,* 197-206.

Jones, J. L., & Kaschak, M. P. (2013). Global statistical learning in a visual search task. *Journal of Experimental Psychology: Human Perception and Performance, 38,* 152-160.

Juan, C. H., Campana, G., & Walsh, V. (2004). Cortical interactions in vision and awareness: hierarchies in reverse. *Progress in Brain Research, 144,* 117-130.

Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin, 70,* 387-403.

Keulen, R., Adam, J., Fischer, M. H., Kuipers, H., & Jolles, J. (2004). Selective reaching: Distractor effects on movement kinematics as a function of target-distractor separation. *Journal of General Psychology, 131*, 345-363.

Kim, M. S., & Cave, K. R. (1999). Top-down and bottom-up attentional control: On the nature of the interference from a salient distractor. *Perception & Psychophysics, 61*, 1009-1023.

Kimchi, R. (1992). The primacy of wholistic processing and the global/local paradigm: A critical review. *Psychological Bulletin, 112*, 24-38.

Kingstone, A., & Klein, R. (1991). Combining shape and position expectancies: Hierarchical processing and selective inhibition. *Journal of Experimental Psychology: Human Perception & Performance, 17*, 512-519.

Kiss, M., & Eimer, M. (2011). Attentional capture by size singletons is determined by top-down search goals. *Psychophysiology, 48*, 784-787.

Kiss, M., Grubert, A., Petersen, A., & Eimer, M. (2012). Attentional Capture by Salient Distractors during Visual Search is Determined by Temporal Task Demands. *Journal of Cognitive Neuroscience, 24*, 749-759.

Kiss, M., Van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology, 45*, 240-249.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences, 16*, 606-617.

Kramer, A. F., & Jacobson, A. (1991). Perceptual organization and focused attention – the role of objects and proximity in visual processing. *Perception & Psychophysics, 50*, 267-284.

Kristjansson, A., & Campana, C. (2010). Where perception meets memory: A review of repetition priming in visual search tasks. *Attention Perception and Psychophysics, 72,* 5-18.

Krummenacher, J., Müller, H. J., & Heller, D. (2001). Visual search for dimensionally redundant pop-out targets: Evidence for parallel-coactive processing of dimensions. *Perception & Psychophysics, 63,* 901-917.

Lamme, V. A. F., Super, H., & Spekreijse, H. (1998). Feedforward, horizontal, and feedback processing in the visual cortex. *Current Opinion in Neurobiology, 8,* 529-535.

Lamy, D., & Zoaris, L. (2009). Task-irrelevant stimulus salience affects visual search. *Vision Research, 49,* 1472-1480.

Leber, A. B. & Egeth, H. E. (2006). It's under control: Top-down search strategies can override attentional capture. *Psychonomic Bulletin & Review, 13,* 132-138.

Levinthal, B. R., & Franconeri, S. L. (2011). Common-fate grouping as feature selection. *Psychological Science, 22,* 1132-1137.

Liao, H. I., & Yeh, S. L. (2011). Interaction between stimulus-driven orienting and top-down modulation in attentional capture. *Acta Psychologica, 138,* 52-59.

Lien, M. C., Ruthruff, E., & Cornett, L. (2010). Attentional capture by singletons is contingent on top-down control settings: Evidence from electrophysiological measures. *Visual Cognition, 18,* 682-727.

Lu, S., & Han, S. (2009). Attentional capture is contingent on the interaction between task demand and stimulus salience. *Attention, Perception, & Psychophysics, 1,* 1015-1026.

Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology, 31,* 291-308.

Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences, 4*, 432-440.

Mack, A., Tang, B., Tuma, R., Kahn, S., & Rock, I. (1992). Perceptual Organization and Attention. *Cognitive Psychology, 24*, 475-501.

Maljkovic, V., & Nakayama, K. (1994). Priming of popout: I. Role of features. *Memory and Cognition, 22*, 657-672.

Maljkovic, V., & Nakayama, K. (1996). Priming of popout: II. Role of position. *Perception and Psychophysics, 58*, 977-991.

Marr, D. (1980). Visual information processing: The structure and creation of visual representations. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences, 290,* 199-218.

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences, 6,* 255-260.

McKinstry, C., Dale, R., & Spivey, M. J. (2008). Action dynamics reveal parallel competition in decision making. *Psychological Science, 19*: 22-24.

McPeek, R. M. & Keller, E. L. (2001). Short-term priming, concurrent processing, and saccade curvature during a target selection task in the monkey. *Vision Research, 41*, 785-800.

McPeek, R. M., Maljkovic, V., & Nakayama, K. (1999). Saccades require focal attention and are facilitated by a short-term memory system. *Vision Research, 39*, 1555-1566.

McPeek, R. M., Skavenski, A., & Nakayama, K. (2000). Concurrent processing of saccades in visual search. *Vision Research, 40,* 2499-2516.

McSorley, E., & Findlay, J. M. (2003). Saccade target selection in visual search: Accuracy improves when more distractors are present. *Journal of Vision, 3(11)*: 20.

McSorley, E., Haggard, P., & Walker, R. (2004). Distractor modulation of saccade trajectories: Spatial separation and symmetry effects. *Experimental Brain Research, 155*, 320-333.

Melcher, D., Papathomas, T. V., & Vidnyanszky, Z. (2005). Implicit attentional selection of bound visual features. *Neuron, 46,* 723-729.

Mounts, J. R. W. (2000). Attentional capture by abrupt onsets and feature singletons produces inhibitory surrounds. *Perception & Psychophysics, 62*, 1485-1493.

Muggleton, N. G., Kalla, R., Juan, C. H., & Walsh, V. (2011). Dissociating the contributions of human frontal eye fields and posterior parietal cortex to visual search. *Journal of Neurophysiology, 105*, 2891-2896.

Müller, H. J., Geyer, T., Zehetleitner, M., & Krummenacher, K. (2009). Attentional capture by salient color singleton distractors is modulated by top-down dimensional set. *Journal of Experimental Psychology: Human Perception and Performance, 35*, 1-16.

Müller, H. J., Heller, D., & Ziegler, J. (1995). Visual search for singleton feature targets within and across feature dimensions. *Perception and Psychophysics, 57*, 1-17.

Müller, H. J., & Krummenacher, J. (2006). Visual search and selective attention. *Visual Cognition, 14*, 389-410.

Müller, H. J., & Rabbitt, P. M. A. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception & Performance, 15*, 315-330.

Müller, H. J., Reimann, B., & Krummenacher, J. (2003). Stimulus-driven and expectancy-driven effects in dimensional weighting. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 1021-1035.

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual-attention. *Vision Research, 29,* 1631-1647.

Navon, D. (1977). Forest Before Trees: The Precedence of Global Features in Visual Perception. *Cognitive Psychology, 9,* 353-383.

Neggers, S. F. W., van der Lubbe, R. H. J., Ramsey, N. F., & Postma, A. (2006). Interactions between ego- and allocentric neuronal representations of space. *Neuroimage, 31,* 320-331.

Nitsche, M. A. & Paulus, W. (2001). Sustained excitability elevations induced by transcranial DC motor cortex stimulation in humans. *Neurology 57,* 1899-1901.

Nitsche, M. A., Schauenburg, A., Lang, N., Liebetanz, D., Exner, C., Paulus, W., & Tergau, F. (2003). Facilitation of Implicit Motor Learning by Weak Transcranial Direct Current Stimulation of the Primary Motor Cortex in the Human. *Journal of Cognitive Neuroscience 15,* 619-626.

Noesen, B., Lien, M. C., & Ruthruff, E. (2014). An electrophysiological study of attention capture by salience: Does rarity enable capture? *Journal of Cognitive Psychology, 26,* 346-371.

Notturno, F., Marzetti, L., Pizzella, V., Uncini, A., & Zappasodi, F. (2014). Local and remote effects of transcranial direct current stimulation on the electrical activity of the motor cortical network. *Human Brain Mapping, 35,* 2220-2232.

Ogawa T, & Komatsu H. (2004). Target selection in area V4 during a multidimensional visual search task. *Journal of Neuroscience, 24,* 6371-6382.

Oliva, A. & Torralba, A. (2007). The Role of Context in Object Recognition. *Trends in Cognitive Sciences, 11,* 520-527.

Olivers, C. N. L., & Eimer, M. (2010). On the difference between working memory and attentional set. *Neuropsychologia, 49,* 1553-1558.

Ostry, D. J., Darainy, M., Mattar, A. A, G., Wong, J., & Gribble, P. L. (2010). Somatosensory Plasticity and Motor Learning. *Journal of Neuroscience, 30,* 5384-5393.

Palmer, J., Huk, A. C., & Shadlen, M. N. (2005). The effect of stimulus strength on the speed and accuracy of a perceptual decision. *Journal of Vision, 5*(5), 376-404.

Palmer, S., & Rock, I. (1994). Rethinking perceptual organization: The role of uniform connectedness. *Psychonomic Bulletin & Review, 1,* 29-55.

Paulignan, Y., MacKenzie, C. L., Marteniuk, R. G., & Jeannerod, M. (1991). Selective perturbation of visual input during prehension movements: 1. The effects of changing object position. *Experimental Brain Research, 83,* 502-512.

Pinto, Y, Olivers, C. N. L., & Theeuwes, J. (2005). Target uncertainty does not lead to more distraction by singletons: Intertrial priming does. *Perception & Psychophysics, 67,* 1354-1361.

Poisson, M. I., & Wilkinson, F. (1992). Distractor ratio and grouping processes in visual conjunction search. *Perception, 21,* 21-38.

Proulx, M. J. (2010). Size matters: Large objects capture attention in visual search. *PLoS One, 5,* e15293.

Reis, J., Schambra H. M., Cohen, L. G., Buch, E. R., Fritsch, B., Zarahn, E., Celnik, P. A., & Krakauer, J. W. (2009). Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. *Proceedings of the National Academy of Sciences of the USA, 106,* 1590-1595.

Resulaj, A., Kiani, R., Wolpert, D.M., & Shadlen, M.N. (2009). Changes of mind in decision-making. *Nature, 461,* 263-268.

Robertson, E. M. (2007). The Serial Reaction Time Task: Implicit Motor Skill Learning? *Journal of Neuroscience, 27,* 10073-10075.

Roy, A., Paulignan, Y., Farnè, A., Jouffrais, C., & Boussaoud, D. (2000). Hand kinematics during reaching and grasping in the macaque monkey. *Behavioral Brain Research, 117,* 75-82.

Rutishauser, U., & Koch, C. (2007). Probabilistic modeling of eye movement data during conjunction search via feature-based attention. *Journal of Vision, 7(6)*: 5.

Sagi, D., & Julesz, B. (1987). Short-Range Limitation on Detection of Feature Differences. *Spatial Vision, 2,* 39-49.

Saleh, M., Reimer, J., Penn, R., Ojakangas, C. L., & Hatsopoulos, N. G. (2010). Fast and Slow Oscillations in Human Primary Motor Cortex Predict Oncoming Behaviourally Relevant Cues. *Neuron, 65,* 461-471.

Saunders, J., & Knill, D. C. (2003). Humans use continuous feedback from the hand to control reaching movements, *Experimental Brain Research, 152,* 341-352.

Schreij, D., Owens, C., & Theeuwes, J. (2008). Abrupt onsets capture attention independent of top-down control settings. *Perception & Psychophysics, 70,* 208-218.

Schubö, A. (2009). Salience detection and attentional capture. *Psychological Research, 73,* 233-243.

Schubotz, R. I. (2007). Prediction of external events with our motor system: towards a new framework. *Trends in Cognitive Science, 11,* 211-218.

Schubotz, R. I., & von Cramon, D. Y. (2002). Predicting Perceptual Events Activates Corresponding Motor Schemes in Lateral Premotor Cortex: An fMRI Study. *NeuroImage, 15,* 787-796.

Schyns, P. G., & Oliva, A. (1994). From Blobs to Boundary Edges: Evidence for Time- and Spatial-Scale Dependent Scene Recognition. *Psychological Science, 5,* 195-200.

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual Reviews of Neuroscience, 33,* 89-108.

Smith, P. L., & Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends in Neurosciences, 27,* 161-168.

Song, J. H., & McPeek, R. M. (2009). Eye-Hand Coordination During Target Selection in a Pop-Out Visual Search. *Journal of Neurophysiology, 102*, 2681-2692.

Song, J. H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *Journal of Vision, 6(9)*: 11.

Song, J. H., & Nakayama, K. (2007). Automatic adjustment of visuomotor readiness. *Journal of Vision, 7(5)*: 2.

Song, J. H., & Nakayama, K. (2008). Numeric comparison in a visually-guided manual reaching task. *Cognition, 106,* 994-1003.

Song, J. H., & Nakayama, K. (2008). Target selection in visual search as revealed by movement trajectories. *Vision Research 48,* 853-861.

Song, J. H., & Nakayama, K. (2009). Hidden cognitive states revealed in choice reaching tasks. *Trends in Cognitive Sciences, 13,* 360-366.

Song, J. H., Rafal, R. D., & McPeek, R. M. (2011). Deficits in reach target selection during inactivation of the midbrain superior colliculus. *Proceedings of the National Academy of Sciences of the USA, 108,* 1433-1440.

Spiegel, D. P., Hansen, B. C., Byblow, W. D., & Thompson, B. (2012). Anodal Transcranial Direct Current Stimulation Reduces Psychophysically Measured Surround Suppression in the Human Visual Cortex. *Plos One, 7*: e36220.

Spivey, M. J., Grosjean, M., & Knoblich, G. (2005). Continuous attraction toward phonological competitors. *Proceedings of the National Academy of Sciences of the USA, 102,* 10393-10398.

Sternberg, S. (1969). The discovery of processing stages. *Acta Psychologica, 30,* 276-315.

Stewart, B. M., Baugh, L. A., Gallivan, J. P., & Flanagan, J. R. (2013). Simultaneous encoding of the direction and orientation of potential targets during reach planning: evidence of multiple competing reach plans. *Journal of Neurophysiology, 110,* 807-816.

Strauss, S., & Heinke, D. (2012). A robotics-based approach to modeling of choice reaching experiments on visual attention. *Frontiers in Psychology, 3*: 105.

Strauss, S., Woodgate, P. J. W., Sami, S., & Heinke, D. (in submission). Attentional guidance by movement-relevant perceptual representations in the human motor cortex. *Neural Networks, in submission.*

Taylor, P. C. J., Muggleton, N. G., Kalla, R., Walsh, V., & Eimer, M. (2011). TMS of the right angular gyrus modulates priming of pop-out in visual search: combined TMS-ERP evidence. *Journal of Neurophysiology, 106,* 3001-3009.

Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics, 51,* 599-606.

Theeuwes, J. (2004). Top-down search strategies cannot override attentional capture. *Psychonomic Bulletin & Review, 11,* 65-70.

Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica, 135,* 77-99.

Theeuwes, J. (2010b). Top-down and bottom-up control of visual selection: Reply to commentaries. *Acta Psychologica, 135*, 133-139.

Theeuwes, J., Olivers, C. N. L., & Belopolsky, A. V. (2010). Stimulus-driven capture and contingent capture. *WIREs Cognitive Science, 1*, 872-881.

Theeuwes, J., Reimann, B., & Mortier, K. (2006). Visual search for featural singletons: No top-down modulation, only bottom-up priming. *Visual Cognition, 14,* 466-489.

Thomson D. R., D'Ascenzo M., & Milliken B. (2013). Learning what to expect: context-specific control over intertrial priming effects in singleton search. *Memory and Cognition, 41,* 533-546.

Torralba, A., Oliva, A., Castelhano, M., & Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: the role of global features in object search. *Psychological Review, 113*, 766-786.

Tsal, Y. & Makovski, T. (2006). The attentional white bear phenomenon: The mandatory allocation of attention to expected distractors locations. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 351-363.

Turatto, M., & Galfano, G. (2001). Attentional capture by color without any relevant attentional set. *Perception & Psychophysics, 63*, 286-297.

Utochkin, I. S. (2013). Visual search with negative slopes: the statistical power of numerosity guides attention. *Journal of Vision, 23(13)*: 3.

Walthew, C. E., & Gilchrist, I. D. (2006). Target location probability effects in visual search: an effect of sequential dependencies. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 1294-1301.

Wertheimer, M. (1923). Laws of organization in perceptual forms. First published as Untersuchungen zur Lehre von der Gestalt II, in *Psycologische Forschung*, *4*, 301-350. Translation published in Ellis, W. (1938). *A source book of Gestalt psychology* (pp. 71-88). London: Routledge & Kegan Paul.

Williams, D. E., & Reingold, E. M (2001). Preattentive guidance of eye movements during triple conjunction search tasks: The effects of feature discriminability and saccadic amplitude. *Psychonomic Bulletin & Review, 8,* 476-488.

Wolfe, J. M. (1994). Guided search 2.0: A revised model of visual search. *Psychonomic Bulletin & Review, 1,* 202–238.

Wolfe, J. M. (2007). Guided Search 4.0, Current Progress With a Model of Visual Search. In Gray, W. (Ed), *Integrated Models of Cognitive Systems* (pp. 99-119). New York: Oxford.

Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided Search: An Alternative to the Feature Integration Model for Visual Search. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 419-433.

Woodgate, P. J. W., Strauss, S., Sami, S., & Heinke, D. (2015). Motor Cortex Guides Selection of Predictable Movement Targets. *Behavioural Brain Research, 287,* 238-246.

Woodworth, R. S. (1899). The accuracy of voluntary movement. *Psychological Review, 3,* (3, Suppl. 13), 1-119.

Yantis, S., & Egeth, H. (1999). On the distinction between visual salience and stimulus-driven attentional capture. *Journal of Experimental Psychology: Human Perception & Performance, 25*, 661-676.

Zach, N., Inbar, D., Grinvald, Y., Bergman, H., & Yaadia, E. (2008). Emergence of Novel Representations in Primary Motor Cortex and Premotor Neurons during Associative Learning. *Journal of Neuroscience 28*, 9545-9556.

Zehetleitner, M., Hegenloh, M., & Müller, H. J. (2011). Visually guided pointing movements are driven by the salience map. *Journal of Vision, 11(1)*: 24.

Zehetleitner, M., Koch, A. I., Goschy, H., & Müller, H. J. (2013). Salience-Based Selection: Attentional Capture by Distractors Less Salient Than the Target. *PLoS One, 8*, e52595.

Zehetleitner, M., Krummenacher, J., & Müller, H. J. (2009). Co-activation - neither serial exhaustive nor interactive - models can explain violations of the race model in visual pop-out search. *Attention, Perception, & Psychophysics, 71*, 1739-1759.

Zehetleitner, M., Proulx, M., & Müller, H. J. (2009). Additional-singleton interference in efficient visual search: A common salience route for detection and compound tasks. *Attention, Perception, & Psychophysics, 71*, 1760-1770.

Zelinsky, G., Rao, R., Hayhoe, M., & Ballard, D. (1997). Eye movements reveal the spatio-temporal dynamics of visual search. *Psychological Science, 8*, 448-453.

Zhang, W., & Luck, S. J. (2009). Feature-Based Attention Modulates Feedforward Visual Processing. *Nature Neuroscience, 12*, 24-2.

Zohary, E., & Hochstein, S. (1989). How serial is serial processing in vision? *Perception, 18*, 191-200.